POPULATION STRUCTURE, SITE FIDELITY, AND FINE-SCALE HABITAT USE OF THE BROADNOSE SEVENGILL SHARK, *NOTORYNCHUS CEPEDIANUS*AT PYRAMID ROCK, FALSE BAY, SOUTH AFRICA

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Declaration

I, Robert Nicholas Vause Raw, know the meaning of plagiarism and declare that all the work in the document, save for that which is properly acknowledged, is my own.

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Abstract

As human impacts on the oceans intensify, it is becoming increasingly important to understand the ecosystems and the species within it, to ensure conservation and management. Apex predators play a key role in the balance of an ecosystem and as such should be a conservation priority.

The broadnose sevengill shark, *Notorynchus cepedianus*, is a large apex predator with a broad distribution in cool-temperate waters. Despite their high trophic position and presumed importance to coastal ecosystems, much remains unknown about the species, leading it to be declared as Data-Deficient on the IUCN Red List. As a result, the species is largely overlooked in conservation management of fisheries.

The aims of this study were to investigate elements of the demographics, fine-scale habitat use and site fidelity of sevengill sharks. The study was conducted at an aggregation hotspot within a Marine Protected Area, near Miller's Point in False Bay, South Africa. This local abundance of sevengill sharks and ease of direct observations makes this site ideal for observational studies of the species. Observations were made by divers who recorded individual shark IDs with digital photographs for subsequent identification. The underlying habitat at the time of data capture was also recorded from photographs. Cormack-Jolly-Seber models were applied to mark-recapture data to determine survival, recapture probability and transience in the population, while the distribution of resightings was analysed to investigate levels of site fidelity.

Over the course of the study 587 individuals were identified from 1119 photographs. No seasonality was observed in shark abundances, contrary to anecdotal observations of the species elsewhere and at the study site. Sex ratios of the population were found to be heavily skewed towards females, with a male : female ratio of 1:4.1.

Survival estimates were constrained by transience, producing an estimate of 59% for transients and 96% for non-transients, while recapture probabilities varied over time, with peaks in spring and summer. The population at the site exhibited a high level of transience, with the majority of individuals only remaining within the area for short periods. This resulted in a high turnover rate of individuals visiting the site and low site fidelity. Females displayed higher levels of site fidelity (75% resighted within six months) than males (only 10% resighted within six months), staying in the area for longer periods and returning more frequently.

Habitat use was found to favour sandy, cobblestone and rocky micro-habitats. If the species is using this aggregation site for protection from predators while resting during the day, it is likely that the use of these micro-habitats allows the sharks unobstructed movement through the site, while still benefiting from the shelter offered by the complex habitat.

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Chapter 1 –Sevengill Sharks, *Notorynchus cepedianus*

1.1 – Taxonomy and distribution

All sharks belong to the taxonomic class Chondrichthyes and are characterized by a flexible, cartilaginous skeleton, true upper and lower jaws, paired fins and nostrils below their head (Compagno *et al.* 2005). Chondrichthyes comprises of two sub-classes, Holocephali (Chimaeras) and Elasmobrachii, to which all other sharks and rays belong. Sharks are then separated from skates and rays at super-order level. Two super-orders exist, the Batoides (skates and rays) and Euselachii (sharks). There are eight orders within the Selachii, comprising of 30 different families (Figure 1.1) and about 500 species (Ebert & Winton 2010).

Notorynchus cepedianus belongs to the order Hexanchiformidae, which consists of only two families, the Chlamydoselachidae or frilled sharks, and Hexanchidae or cow sharks. The family Hexanchidae comprises three extant genera and only four extant species: the broadnose sevengill shark, *Notorynchus cepedianus,* the sharpnose sevengill shark, *Heptranchia sperlo*, the bluntnose sixgill shark, *Hexanchus griseus* and the bigeye sixgill shark, *Hexanchus nakamurai*. The Hexanchidae are characterised by the presence or six or seven gill slits and only one dorsal fin (Figure 1.2).

Teeth also play a role in identifying members of the Hexanchidae. Upper and lower jaws are well differentiated, with upper anterolateral teeth being small and narrow with a main cusp often with smaller cusplets. The lower anterolateral teeth are very broad, compressed and saw-like in appearance, with a series of large cusplets and a short to elongated cusp (Figure 1.3, Compagno 1984). Early Hexanchid evolution has been inferred from isolated teeth found in Jurassic marine deposits in Europe and complete specimens in Germany (Long *et al.* 1993). The earliest known records of the Hexanchidae date back to the early Jurassic, with a partial tooth of an unidentifiable hexanchid having been uncovered from sediments in southern Sweden (Rees 2000), while the earliest New World occurrence of the family is reported from the Late Aptian strata of northern California (Long *et al.* 1993).

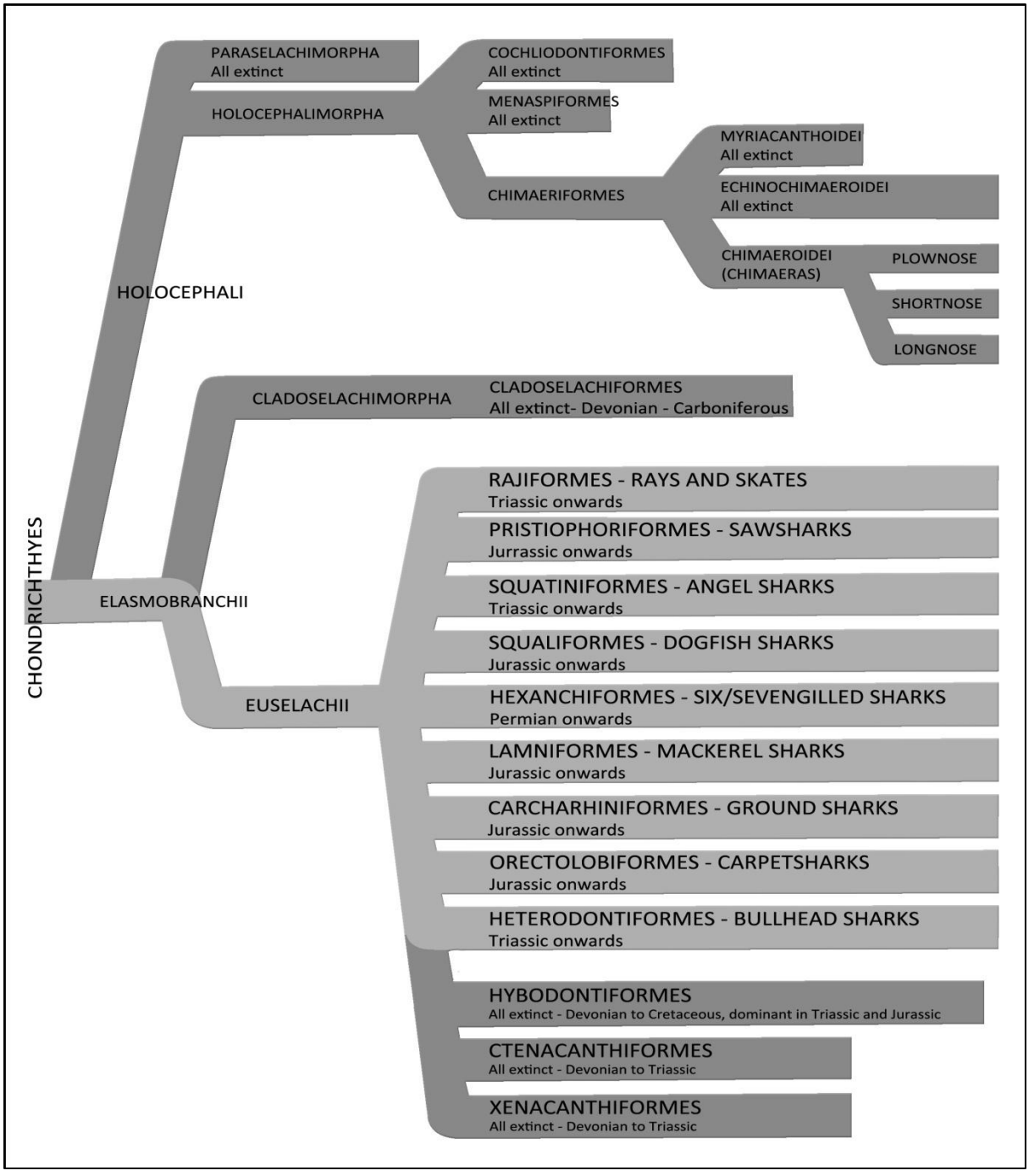


Figure 1.1: Family tree of Chondrichthyes (From Compagno *et al.*2005).

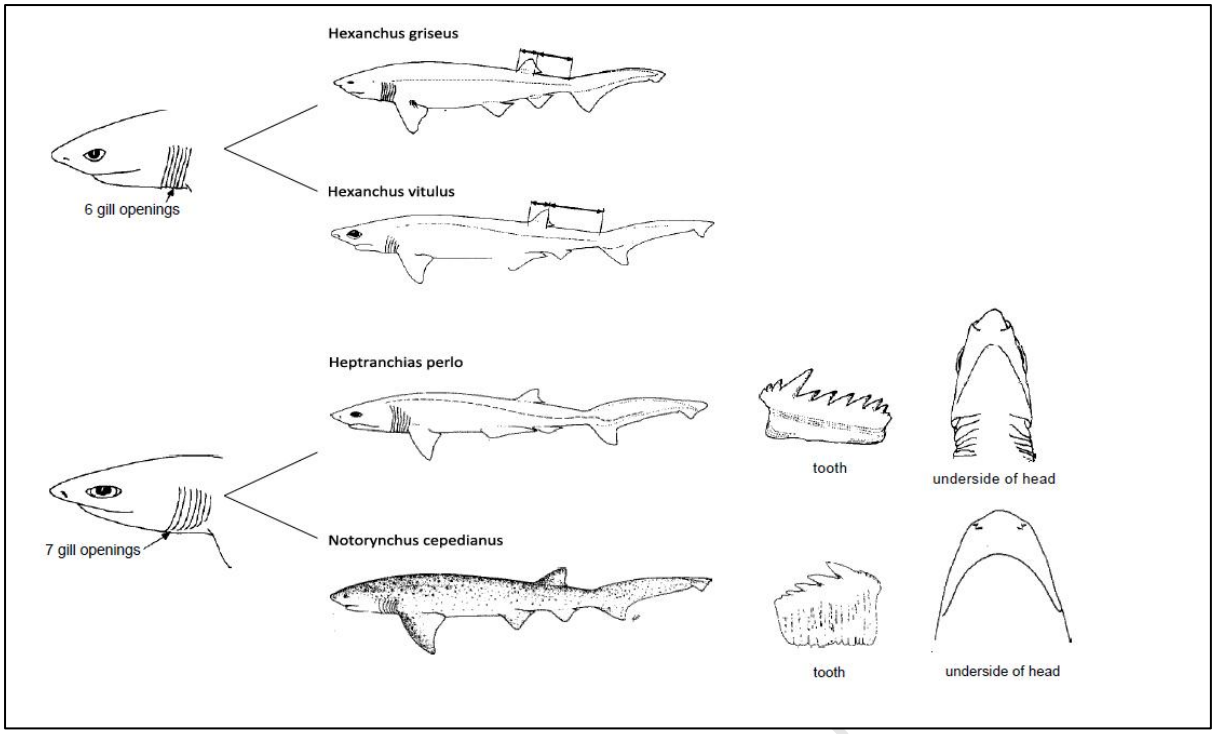


Figure 1.2: General form and identifying features of the four extanct Hexanchidae species (From Compagno 1984).

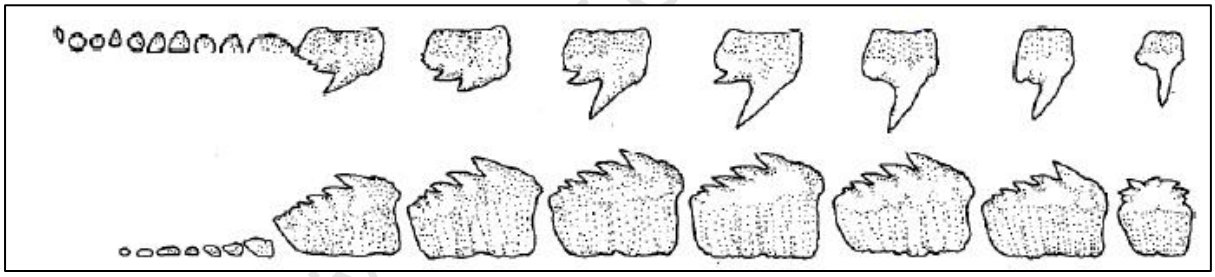


Figure 1.3: Upper and lower right side teeth of the sevengill shark (From Compagno 1984).

The broadnose sevengill shark, *Notorynchus cepedianus,* is the only species in the genus *Notorynchus* and can be identified as being a broad headed, small-eyed, seven-gilled shark, with a single dorsal fin and numerous black spots on the body (Figure 1.2, Compagno 1984).

1.1.2– Distribution and habitat

The broadnose sevengill shark is a relatively large, predatory shark with a fairly broad distribution (Figure 1.4), found predominately in cool-temperate waters in both the northern and southern hemispheres, with no confirmed records from the tropics (Barnett *et al*. 2012). They are most abundant in water temperatures ranging between 12 and 18°C (Van Dykhuizen & Mollet 1992). In the eastern Pacific, sevengill sharks range from south-eastern Alaska to the Gulf of California and along the coasts around Mexico, Peru and Central Chile. In the western Pacific, their range includes Siberia, southern Japan, the Koreas, Taiwan, China, Vietnam, Australia and New Zealand. In the western south Atlantic, the species has been reported around Southern Brazil, Uruguay and Northern Argentina, while in the eastern south Atlantic and Indian Oceans, the species has been observed around Namibia, South Africa and Tristan da Cunha with unconfirmed reports from India and Sri Lanka (Campagno1984, 2005).

Around southern Africa, sevengill sharks are one of the most commonly occurring species of shark in temperate coastal waters, ranging from East London on the east coast, to Möwe Bay on the west coast in Namibia (Ebert 1991b, 1996; see Figure 2.1).

Sevengill sharks are a distinctly coastal species, often inhabiting bays and harbours (Compagno 1984, Ebert 1991b) but are recorded to dive to depths of greater then 200m (Barnett pers. com.) and are the only species within the Hexanchidae that exclusively inhabit coastal and shelf waters (Compagno 1984, Luciflora *et al.* 2005).

Figure 1.4: Global distribution of sevengill sharks (From IUCN, Compagno 2005).

1.2 –Diet and feeding

1.2.1 – Diet

Sevengill shark are a eurytrophic predator that optimises available resources and are capable of feeding on a wide range of prey, including pinnipeds, other sharks, batoids, cephalopods, cetaceans and teleosts (Ebert 1989, 1991b, 2002, Lucifora *et al.* 2005, Braccini 2008, Barnett *et al.* 2010b). In the Western Cape, the sevengill shark diet has been found to consist primarily of chondrichthyans, constituting over 70% by mass, with marine mammals accounting for a further 20% (Ebert 1991b, Braccini 2008). The importance of chondrichthyans in the diet of sevengill sharks is demonstrated by the presence of no less than 13 species of chondrichthyans in the diet along the coast of South Africa (Ebert 1989).

Ontogenetic changes in the diet of sevengill sharks have been observed (Ebert 2002, Lucifora *et al.* 2005), the general trend being from teleost fish dominating in smaller individuals to larger chondrichthyans and marine mammals becoming increasingly consumed by larger size classes (Ebert 2002). Only the largest individuals feed on large mammalian prey, such as adult South American sea lions *Otaria flavescens* (Lucifora *et al.* 2005).

Since they feed largely on chondrichthyan, teleost and marine mammal species, sevengill sharks can be considered apex predators within near-shore coastal ecosystems, with the white shark, *Carcharodon carcharias,* being the only trophic equivalent in the areas in which they co-occur (Ebert 1991a). Although juveniles may fall prey to larger teleosts, seals and other sharks, once they reach adulthood, white sharks and killer whales, *Orcinus orca*, are possibly their only predators (Ebert 1991b).

1.2.2 – Feeding

Sevengill sharks are versatile predators, able to employ a diverse range of feeding strategies to accommodate their diverse diet, which includes both slow and fast-moving prey. The frequency with which fast-moving prey are found in the diet suggests that the presence of such prey is not simply a result of scavenging, but rather of active hunting (Ebert 1991a). Ebert (1991a) suggests four basic foraging strategies used by sevengill sharks: burst of speed, ambush, stealth and social facilitation. The burst of speed strategy is characterised by initial lethargic swimming, punctuated by a sudden burst of speed to capture a prey item. Both ambush and stealth strategies occur under conditions of poor visibility (including low-light and nocturnal hunting), when a predator may approach a prey item without detection. Social facilitation may allow sevengill sharks to target larger prey, such as the Cape fur seal (weighing up to 350 kg), than would be possible for an individual to subdue. Spy-hopping has been observed in sevengill sharks, although the purpose of this behaviour is not fully understood. Ebert (1991a) suggests this behaviour is unlikely to be used for predator avoidance, and rather as a means of prey detection. Most prey of sevengill sharks is found to be sectioned before swallowing, with only the smallest prey being swallowed whole (Ebert 1991a, Lucifora *et al.* 2005).

Prey availability may influence the feeding behaviour of sevengill sharks, with the ability to feed on both small and large prey allowing this species to exploit a wide range of food resources (Ebert 1991a). Barnett *et al.* (2010b) suspect there may be a connection between plentiful resources and sevengill shark diet, with temporal variation in diet relating to variation in prey abundance. Sevengill sharks may move into coastal areas as they know prey is there, however, they may also be versatile, opportunistic predators exploiting resources available in a region for only a short period of time, switching their diet to a food source as it becomes available in the area.

While differences in prey abundances between different areas appear to influence the relative prey consumption rates of sevengill sharks, to fully understand preferential prey choice, relative abundance estimates are needed for all possible prey items. As Barnett *et al.* (2010b) only sampled some of the most common prey items, caution is needed in the interpretation of these results.

Studies on captive animals (van Dykhuizen & Mollet 1992) suggest that adult sevengill sharks require very little food in captivity to meet their daily metabolic requirements (0.2% body weight, (BW), day^{-1}). Juveniles, however, required far greater amounts of food (up to 2% BW day^{-1}) than adults. These findings are supported in wild populations, where juveniles have been observed to have higher rates of prey consumption than adults (Lucifora *et al.* 2005). Age is therefore considered an important factor determining food intake of sevengill sharks, while other factors, including feeding cycles, previous meal size, rates of digestion, gastric evacuation and water temperatures are also considered to affect food consumption in sharks (van Dykhuizen & Mollet 1992).

1.3 – Life history

Fairly little is known about the life history of sevengill sharks, with even greater gaps existing in the knowledge of population demographics and movement patterns of the species (Stevens *et al.* 2000).

1.3.1 – Growth and aging

The sevengill shark is generally a slow-growing species, although large gaps exist in the literature regarding growth rates of the species. Ebert (1989) reported that none of the methods involving the use of vertebrae to age an individual were successful in this species, due to the lack of calcification in the vertebrae, leading to difficulties in aging individuals caught in the wild and hindering estimates of growth. Tag-Recapture studies have also yielded low success rate in producing growth rate data (Ebert 1996), but see Braccini *et al.* (2010).

Studies of captive sevengill sharks have shown newborns to exhibit fairly rapid growth rates during the first few years of life (Figure 1.5, Van Dykhuizen & Mollet 1992), although faster growth of juveniles observed in laboratory studies has often been interpreted to simply suggest that faster growth rates occur in captive animals (Natanson & Cailliet 1986). Van Dykhuizen & Mollet (1992) argue that the faster growth rates observed in captive juveniles were not a result of having been raised in captivity, but were rather because younger sharks grow faster than older ones (Carrier and Leur 1990) and that growth rates can be easily misinterpreted if strict attention is not paid to age. Based on comparisons with the limited field data available, Van Dykhuizen & Mollet (1992) concluded that growth rates of sevengill sharks observed in captivity are similar to growth rates in the wild.

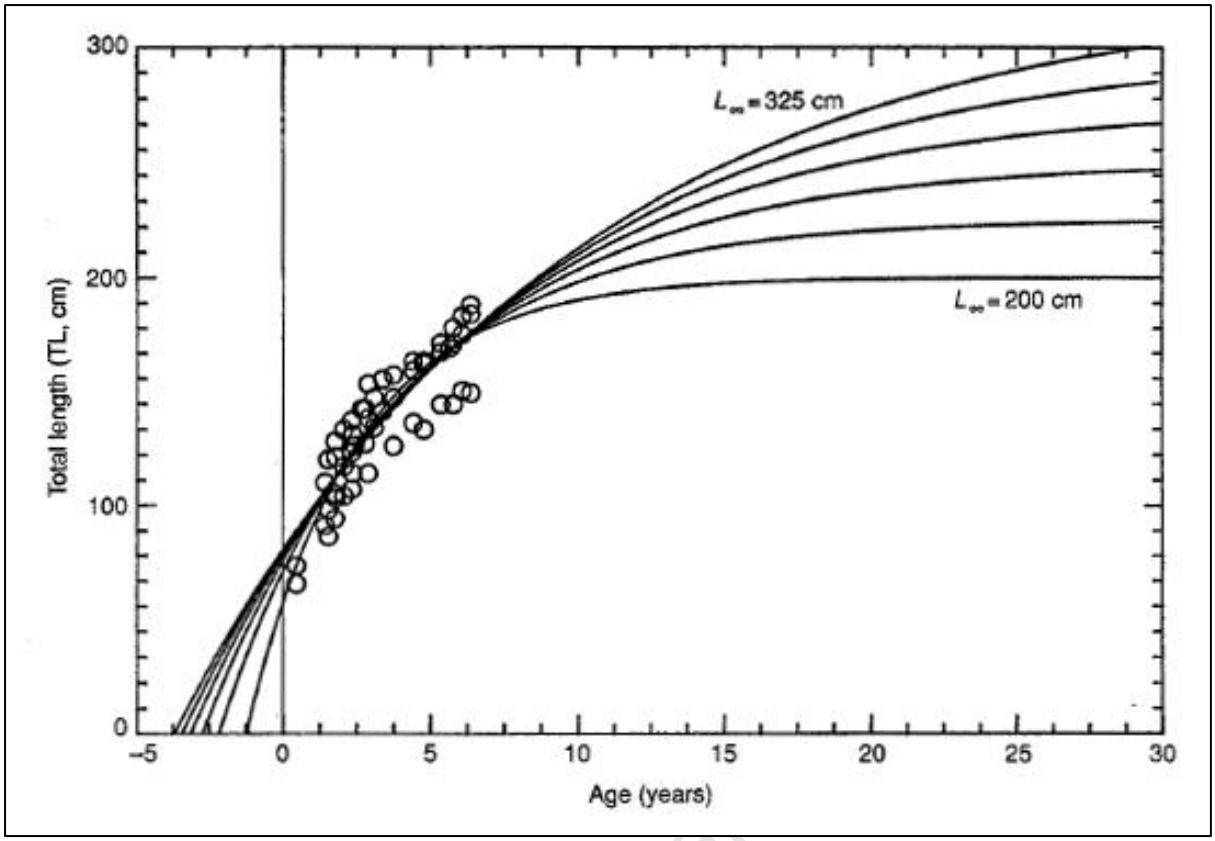


Figure 1.5: Exponential regression of total length (TL) on estimated age, based on estimated age of juvenile sevengill sharks in captivity (From Van Dykhuizen and Mollet 1992).

Braccini *et al*. (2010) argue against this, again using the argument that juveniles in captivity grow faster than those in the wild and that no data on adult males were used in the growth models produced by Van Dykhuizen & Mollet (1992). Having used a wider size range of both captive and wild female sevengill sharks, Braccini *et al.* (2010) found that female sevengill sharks do in fact grow faster in captivity than in the wild.

Using stochastic versions of the von Bertalanffy–Fabens growth model, accounting for heterogeneity in individual growth of both juvenile and adult sevengill sharks in captivity, as well as in the wild, Braccini *et al*. (2010) provide a more biologically comprehensive representation of growth. This method produced estimates of total length (TL) for wild males (272-283 cm TL) that are similar to the maximum reported size of wild males (242 cm TL, Ebert 1990, as cited in Braccini *et al.* 2010). Estimates for wild females (348-386 cm TL) were higher than the reported maximum size (~300 cm TL, Last and Stevens 1994), although Braccini *et al*. (2010) suggest that there is building

evidence from fisheries to suggest that females can grow beyond 300 cm TL, although the source of this evidence is not mentioned (Braccini, unpublished). Estimates of growth for smaller sharks (50 cm TL) derived from these growth models predicted an annual growth of 22 cm for wild males and 26 cm for wild females, which are similar to growth of neonates observed in the field (25-35 cm, Ebert unpublished data).

This study, however, is limited by the fact that data were pooled from different aquaria for captive sharks, and from a wide geographical range for wild sharks. In doing this, the assumption of no variability in rearing conditions between the two aquaria and no variability in the environmental conditions between geographical ranges had to be made. However, sevengill sharks show phenotypic plasticity in growth, suggesting that differences in the environmental and feeding conditions would, in fact, translate into difference in growth, impeding the strength of this study (Braccini *et al.* 2010).

1.3.2 – Maturity and reproduction

1.3.2.1 – Male maturity

Maturation in male sevengill sharks is defined by six indices (Ebert 1989, 1996):

1. An abrupt change in the slope of the inner clasper length/TL relationship.
2. Development of clasper sac and scroll.
3. An increase in the slope of the testes mass/TL and testes length/TL relationships.
4. The presence of an enlarged, coiled epididymis in mature sharks.
5. The expulsion of sperm through the genital papilla by applying pressure along the sperm sac.
6. Calcification of the terminal cartilage elements.

The size at maturity for male sevengill sharks is taken to be the point at which the species can not only produce viable sperm, but also have sufficient calcification of terminal cartilage elements for reproduction. Initial estimates of size at maturity for males indicated that all individuals over 150

cm TL are mature (Ebert 1989). However, although these animals were internally mature, the intromittent organs (claspers) necessary to transmit sperm to the female were under-developed. Calcification of these organs also coincides with a rapid growth in the length of the claspers, creating a final criterion for distinguishing maturity (Ebert 1996). Taking clasper calcification into account, the length at complete sexual maturity for males has been found to be approximately 165 – 170 cm total length (TL) (Ebert 1996, Lucifora *et al.* 2005). Van Dykhuizen & Mollet (1992) calculated an age at sexual maturity of males as 4.3 - 5.0 y, although estimates were based on captive individuals and it may not be reliable to compare these to wild individuals. However, although reaching maturity, a male of this size may still be at a size disadvantage compared to larger adults, excluding it from the breeding population (Ebert 1996). Smaller individuals may also be physically unable to successfully mate with larger females.

1.3.2.2 – Female maturity

Female maturity is defined using the following criteria:

1. Differentiation of the ovaries and egg development.
2. Rapid increase in the slope of the shell gland width/TL relationship.
3. Wide and pendulous oviducts.
4. The presence of fertilized eggs or embryos in the oviducts.

Individuals entering their first breeding season have oviducts which are narrow and constricted, whereas individuals which have given birth at least once have oviducts which are wide and pendulous. Female sevengill sharks have a prolonged maturation period, entering their first breeding season at a size of between 218 and 244 cm TL (Ebert 1996).

1.3.2.3 – Reproduction

A two year reproductive cycle has been deduced for sevengill sharks (Figure 1.6), based on the staggering of females that enter the breeding population (Ebert 1996). Consecutive, year-long ovarian and gestation cycles mean that at any one breeding season the population consists of

approximately equal number of non-gravid mating females and gravid females about to give birth. Males have viable sperm throughout the year and appear to be capable of reproducing year-round (Ebert 1996). Sevengill sharks are ovoviviparous and highly fecund, with 80 - 100 young born per pregnancy (Ebert 1996, Ebert 2001, Lucifora 2005).

High metabolic requirements of juvenile sharks and the resultant high rates of prey consumption may be a driving factor in the selection of pupping and nursery grounds, with preference for highly productive areas (Lucifora *et al*. 2005). However, very little is known about actual pupping and nursery grounds for the species. Both California and Patagonia are suspected to function as nursery grounds for sevengill sharks (Ebert 1989, Lucifora *et al.* 2005), but no actual nursery grounds have been clarified or quantified for the species, based on the nursery area protocol proposed by Heupel *et al.* (2007). Barnett *et al.* (2010c) found no evidence for either Derwent Estuary or Norfolk Bay to be used as nursery grounds, suggesting that sevengill sharks may not use specific nursery grounds in Tasmania, instead giving birth across their range. Alternatively, nursery areas may be in areas yet to be discovered.

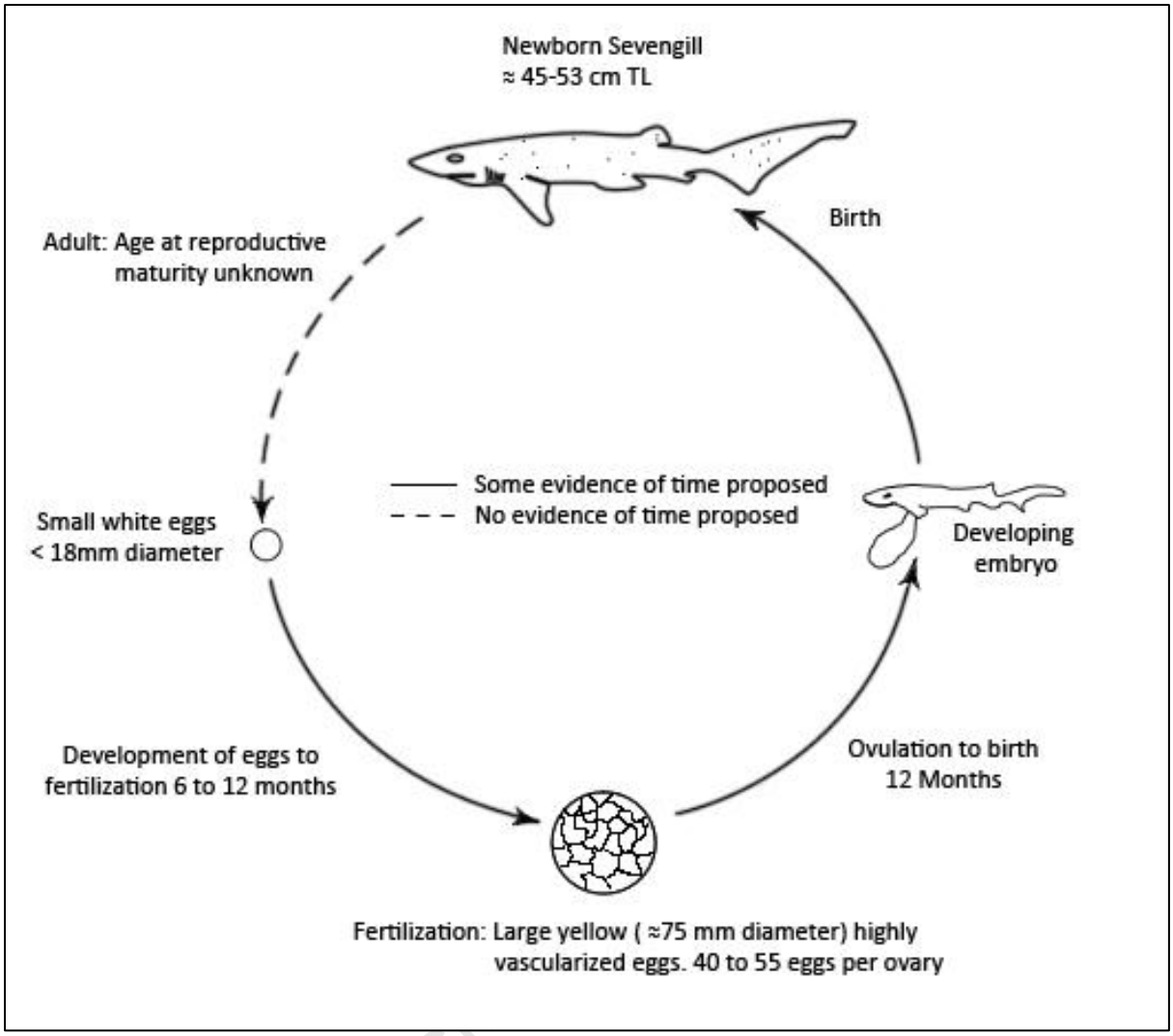


Figure 1.6: Schematic diagram of developmental stages and their proposed timing in the sevengill shark. Length of lines not proportional to times proposed (From Ebert 1989).

1.3.3 – Movement patterns

1.3.3.1 – Long-distance movements and site fidelity

Until recently, the large scale movement patterns of sevengill sharks have remained unclear. Initial theories (Ebert 1996) suggested that although long-range movements are unknown, sevengill sharks do display signs of site fidelity and that individuals will migrate back to the same breeding grounds(Ebert 1996). This, however, was based on a single record of an adult female that was recaptured at the same location in Humboldt Bay, northern California, as the original capture, after being at liberty for approximately 730 d. Further studies using tagging data of 457 individuals

(Barnett *et al.* 2010c) again showed support of site fidelity, this time in south-east Tasmania, with 55 of the 56 recaptures caught in the original tagging location.

Barnett *et al.* (2011) found that sevengill sharks showed both seasonality and site fidelity in the use of two coastal habitats in south-east Tasmania, having used acoustic telemetry to monitor the movements of 43 individual sevengill sharks fitted with acoustic-coded V16 transmitters over two years. The general pattern observed was for sharks to leave the coastal areas during winter and to return during spring/summer. Females appeared in coastal waters earlier than males, arriving in spring, with the males only arriving in early summer. The recapture of animals in the habitat where they were tagged and the low spatial overlap between individuals tagged in each of the two coastal areas suggest site fidelity over relatively fine spatial scales (about 30 km)(Barnett *et al*. 2010c, Barnett *et al*. 2011).

The absence of smaller size classes (<150 cm) of sevengill sharks and lack of any evidence of reproduction in the area eliminates mating, pupping and use of natal sites as the cause of site fidelity. Site fidelity is therefore assumed to be linked to feeding, with high seasonal abundance of known prey species during summer supporting feeding site fidelity (Barnett *et al*. 2010c, 2011).

Data on long-distance movements of sevengill sharks are very limited, although long-term tagging programs are underway, revealing some interesting results. Barnett *et al.* (2011) were able to track the movements of three acoustically tagged males and three PAT tagged males, having moved from their initial tagging location in south-east Tasmania and to a similar vicinity in southern New South Wales, respectively. These movements, together with two PAT-tags released in Bass Strait, suggest a northern seasonal migration by males. The return of two of these acoustically tagged males and one male double tagged with acoustic and PAT-tags to the Tasmanian coastal area adds further support to long-range site fidelity. A northerly migration by males during winter is further supported by catch data in New South Wales, where 80% of the catch comprises males, predominantly caught during August-October (winter-spring), with near absence of sevengill sharks

from catches during summer. Williams *et al.* (2012) collected detailed movement data for 32 acoustically tagged sevengill sharks in and around north-east Pacific Ocean estuarine embayments. The data revealed a distinctly seasonal pattern of estuary use, with individuals moving into Willapa Bay during spring and summer and dispersing to nearshore coastal habitats in autumn. Spatio-temporal of segregation by both size and sex were observed in the Bay, with males and small females using peripheral channels early in the season before joining larger females in the central estuary. Williams *et al.* (2012) noted high degrees of site fidelity to specific sites within an estuary, similar to results observed in Tasmania by Barnett *et al.* (2011).

The migration of females' remains unclear, with added speculation regarding the separation of females during winter, with some individuals migrating out of coastal areas, but others remain within the Derwent Estuary, with one hypothesis suggesting that pregnant individuals move somewhere specifically to pup (Barnett *et al*. 2011). Williams *et al.* (2012) noted that movements of sevengill sharks between estuaries, as far as 1800km from Washington State to California, may support the feasibility of broad-scale coastal movements to known birthing and nursery grounds.

1.3.3.2 – Fine-scale movements

Very little work has been done on fine-scale movements of sevengill sharks, but see Barnett *et al.* (2010d). Early work on the movement of the species was been based on animals tagged and released using fishing methods (Ebert 1996, Barnett *et al.* 2010c) which, although giving useful data on broad-scale movements and site fidelity of the species, lack the resolution required for fine-scale movement studies. Recent studies have begun to use acoustic telemetry to investigate fine-scale movements of sevengill sharks. Barnett *et al.* (2010d) used acoustic telemetry systems to track the location of individual sevengill sharks in Norfolk Bay, Tasmania. Two methods of tracking were used, the first being the VEMCO radio-acoustic positioning system (VRAP), which uses an array of stationary acoustic receivers to triangulate the exact position on tagged individuals. The second involved active tracking the movements of two individuals tagged with pressure-sensitive acoustic transmitters from a vessel using a receiver and directional hydrophone. These methods allowed the

researchers to record fine-scale movements of the species, including exact position, speed and depth.

Results showed distinct differences in activity between night and day. Day-time movement was found to be fairly uniform, appearing slow and sluggish, rarely moving much above the substratum. The movement of these sharks along the bottom during the day could, however, may also be linked to the hunting of marine mammals, allowing individuals to attack prey on the surface from below, as suggested by Ebert (1991a). Night-time movement, in contrast, revealed an oscillatory swimming motion, initiating oscillations from the substratum, ascending into the water column, before returning to the substratum. This oscillatory movement is most likely related to feeding behaviours, allowing sevengill sharks to approach bottom-dwelling prey, such as the Gummy shark *M. antarticus*, skates and urolophids, which are the most common prey items in the area, from above, making use of an ambush strategy in low light conditions to limit the prey's flight response. Alternative hypotheses for the oscillatory movement include searching through the water column for olfactory cues.

Burst speed events were noted both during the day and at night, although differences were found in the depth at which the burst speed events occurred. During the day, all burst speed events observed occurred near the substratum, while at night they occurred higher up the water column. Due to the lack of predators associated with sevengill sharks, the possibility of these events being linked to a flight response was eliminated, suggesting instead that burst speed events are linked to feeding behaviour. Barnett *et al.* (2010d) speculated that periods of reduced movement following a burst speed event could be a resting period following an unsuccessful attack, or the shark was consuming the prey.

Barnett and Semmers (2012), using an array of acoustic receivers set in Norfolk Bay, tracked the fine-scale movements of sevengill sharks and chondrichthyan prey items, to compare spatial movements within their common habitat. Results showed high spatial overlap and similar habitat

use between predator and prey. The abundance of both predator and prey within the Bay, coupled with their similar movement patterns, suggests that sevengill sharks may move into the Bay to exploit abundant resources.

Similarly, Williams *et al.* (2012) used an array of acoustic receivers to analyse fine-scale movements of sevengill sharks in north-eastern Pacific embayments. Their results showed segregation of both size and sex within Willapa Bay, with males and small females using peripheral tributaries early in the season, while females remained concentrated in the central estuary.

1.4 –Threats and conservation

1.4.1 – Threats

Elasmobranch species typically display slow growth, low fecundity and low resilience to exploitation. As a result, over-exploitation is threatening many shark populations world-wide (Stevens *et al.* 2000). Over-fishing has an influence on a number of aspects of shark biology. Apart from causing a decline in the abundance of a species, fishing pressures may cause a shift in size and age structures within populations. Fisheries often target larger individuals, resulting in shifts towards smaller size structures in a population, having significant repercussions for reproductive output (Stevens *et al*. 2000). Sevengill sharks are known to be vulnerable to over-exploitation, with intense inshore fisheries causing a collapse in the central Californian stock in 1980's (Compagno 2005). Similar fishing pressures are expected to be present for most of the specie's distribution (Barnett *et al.* 2012). Worldwide little is known about current population sizes of the species, with no studies to date producing estimates of population size. Regional time series of catch landings are available for U.S.A and Australia, while global level time series data are available from FAO for 1986-2009, however, lack of enforcement and incentives for fisheries management agencies to keep accurate records lead to uncertainty in these data (Barnett *et al.* 2012).

1.4.2 – Interest to fisheries

The large size, local abundance and high quality meat of sevengill sharks make them subject to both sport and commercial fisheries(Compagno 1984).Fishing pressures on this shark are particularly high around the California and Australian coasts, with the flesh being sold for human consumption. The species is also targeted in China for its skin, which is made into leather products, as well as its liver, which produces oil with high concentrations of vitamin A (Compagno 1984, 2000). Sevengill sharks along the Californian coast were among the most common species taken by shark fisheries in the 1930's and 1940's. After this fishery collapsed in the late 1940's, sevengill sharks continued to face pressure, being taken in considerable numbers in fishing competitions in San Francisco Bay (Ebert 2001). The release of the movie Jaws in the 1970's renewed interest in shark fisheries (Ebert 2001), leading to a collapse in the central Californian stock in the 1980's (Compagno *et al.* 2005).

In South Africa, sevengill sharks are targeted by a host of fisheries, including commercial linefish, demersal longline, and gillnet fisheries. A report by the Department of Agriculture, Forestry and Fisheries (DAFF 2010) showed that both offshore and inshore trawl fisheries catch sevengill sharks as bycatch, with the quantity of sharks caught as bycatch often outnumbering those caught by direct demersal longline fisheries. As the availability of other valuable linefish has decreased, there has been a steady increase in the catches of sharks in the linefish industry. While high mercury content in larger sharks limits the value of the meat, the high value of the fins, up to R2500 per kg, acts as a driving force for shark fisheries, including sevengill sharks (DAFF 2010). Despite this, catch rates of sevengill sharks remain fairly low in South African waters, as compared to those of other demersal shark species (Table 1.1).

Sevengill sharks are also a popular target for sports fisheries in South Africa. Sevengill sharks, however, do not appear to handle angling stress very well. This is particularly the case for rock and surf angling, where individuals are often dragged through the surf across rugged shorelines, causing extensive damage and often resulting in mortalities, even when the animal is released after capture (da Silva pers. com.).

Table 1.1: Catches in tons and Catch Per Unit Effort (CPUE) of demersal shark species from 2006 – 2008. From DAFF 2010.

	Catch (tons)			CPUE (kg hook^{-1})		
Species	2006	2007	2008	2006	2007	2008
Soupfin shark (*Galeorhinus galeus*)	6.90	8.39	29.80	1.11	0.72	0.22
Smoothhound shark (*Mustelus mustelus*)	17.11	38.40	17.00	2.56	3.62	0.13
Gully shark (*Triakis megalopterus*)	0.93	1.05	0.00	0.15	1.00	0.00
Copper sharks (*Carcharhinidae*)	8.14	13.80	2.80	1.19	1.35	0.02
Sevengill sharks (*Notorynchus cepedianus*)	**0.05**	**0.25**	**1.80**	**0.01**	**0.02**	**0.01**
Skates	0.58	5.06	1.70	0.13	0.50	0.01

1.4.3 – Conservation

The distinct lack of information regarding sevengill sharks has led to the species being regarded as 'Data-Deficient' on the IUCN Red List (Compagno 2005). In south-eastern Australia, based on reported catches, sevengill sharks are categorized as at high ecological risk in terms of abundance and high risk in terms of catch susceptibility (Walker *et al.* 2007 as cited in Barnett *et al.* 2012), as well as being at high risk in the gillnet sector of the Australian Southern and Eastern Scalefish and Shark Fishery (SESSF), using a rapid quantitative sustainability assessment for fishing effects (Zhou *et al.* 2007, as cited in Barnett *et al.* 2012). Very little is known about the population status of the species, in particular with regard to areas outside of their nursery grounds. While both California (Ebert 1989) and Argentina (Lucifora *et al.* 2005) are suspected to function as nursery grounds for sevengill sharks, no nursery grounds have been clarified or quantified for the species based on the nursery area protocol proposed by Heupel *et al.* (2007).

Due to the lack of data on the species, there is generally no management of fisheries or protection for this species, both locally (da Silva, pers. com.) and internationally (Compagno 2005). Sevengill sharks, however, do occur in at least one marine reserve in South Africa (Compagno 2005). Due to their low commercial value, the demersal longline fishery in South Africa has volunteered to release them alive (da Silva pers. com.), but formal management of the stocks are still required.

1.5 – Motivation for current research

Despite the broad distribution, high trophic position and the important role of sevengill sharks in coastal ecosystems, large gaps still exist in our knowledge of sevengill shark ecology, biology and their role in ecosystems. Contention still exists regarding the relationship between age and size, and consequently age at maturity. Also, while recent work has looked at fine-scale movements, few data exist on the fine-scale habitat use or habitat preference of sevengill sharks. Despite long term fisheries tagging programs, no literature is available on the survival of the species, either regarding life-expectancy, or survival over time when threatened by fisheries or predation. Without proper knowledge of all aspects of the life history of a species, it is difficult to make informed management decisions to prevent a future collapse in populations.

This study looks at a portion of a population of sevengill sharks that aggregate around a small area within a marine protected area in South Africa. This year-round hotspot provides an excellent opportunity to observe this species in its natural environment, without the need for invasive sampling methods. An aggregation such as this has the potential to not only provide valuable insight into elements of the life history of the species, but may also provide insight into population structure, relative abundance, site fidelity and fine-scale habitat use. An understanding of what attracts individuals to this site may provide useful indicators for conservation management.

In this study I provide estimates of the survival probabilities over time of sevengill sharks around an aggregation site. I also investigate seasonality and sex ratios of sevengill sharks, along with short and long term site fidelity and fine-scale habitat use at the aggregation site. From this I provide a base of information to answer questions of when and why individuals of the species aggregate at this site.

Chapter 2 – General Methods

2.1 – Study site

The study was carried out at the Pyramid Rock dive site (area: 0.033km^2, 34°14'12.51"S, 18°28'38.91"E), near Miller's Point, on the western shore of False Bay, South Africa (Figure 2.1). This site has recently been identified as an area where sevengill sharks aggregate year round and can reliably be seen and photographed by SCUBA divers (Kock pers. com). There are no published records of such aggregation sites elsewhere. The site is located in the Table Mountain Marine Protected Area (TMPA) and is classed as a restricted zone, which means that no fishing may take place (no take zone) (Figure 2.2). Characterised by kelp forest habitat, the site contains large rocky outcrops, separated by a series of sandy gullies and cobblestone beds. The mean depth at the study site is 8 m (Range 0 – 14m). Although generally sheltered, a south westerly swell can result in a fair degree of surge and greatly decreased visibility. Depending on the season and local sea conditions, visibility can range from 0 – 25 m.

The site has in recent years become a popular destination for eco-tourism. Regular commercial tour operations began in 2009 and in 2012 at least six dive companies as well as a number of local dive clubs are running regular trips to dive with sevengill sharks at the site.

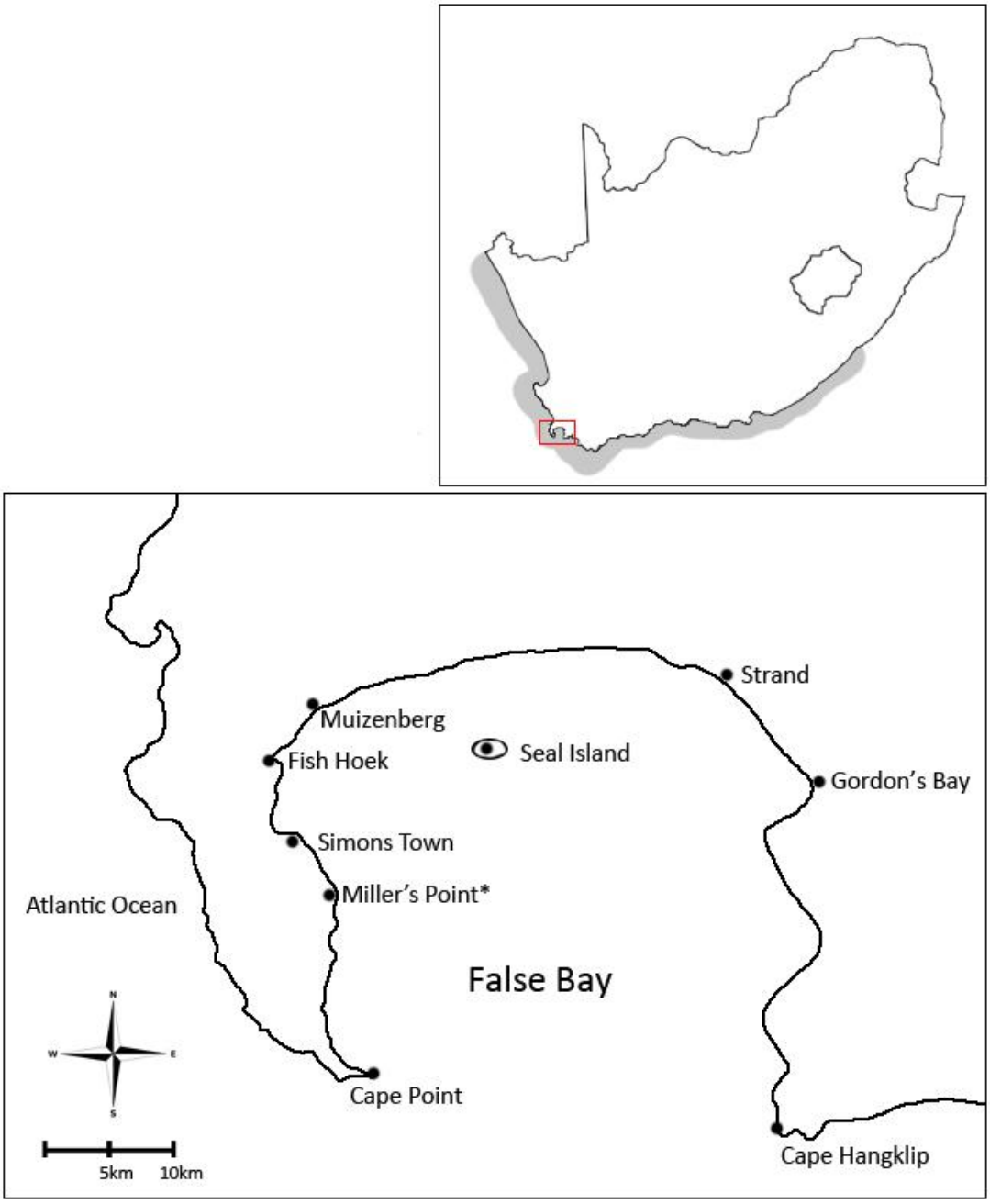


Figure 2.1: Map of South Africa showing the geographic distribution of sevengill sharks (top: shaded). Enlarged map of False Bay shows the location of the Miller's Point study site(*).

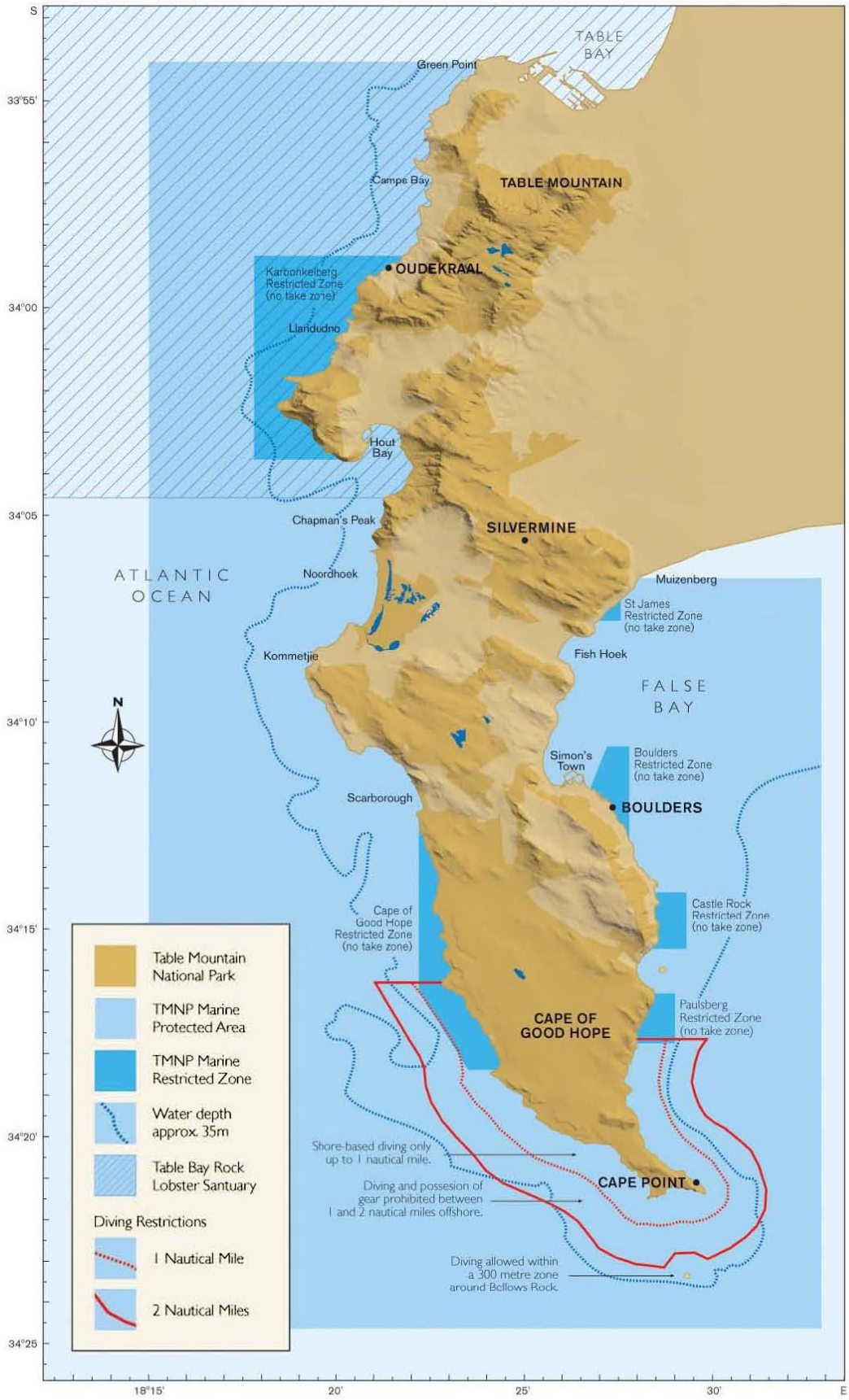


Figure 2.2: Map of Table Mountain Marine Protected Area, showing restricted zones (Pyramid Rock falls in the Castle Rock Restricted Zone). From SANParks (2012).

2.2 – Study design and data collection

2.2.1 Data collection:

Exploratory dives conducted by a commercial diving company over the year preceding the study have allowed the development of local knowledge of shark movements and hotspots. Photographs of individual sharks were taken on an ad-hoc basis by a select group of recreational divers (n=4), as well as by the researchers (n=3). Data were collected on a monthly basis between February 2009 and June 2011, with a three month gap from June – August in 2009 due to unavailability of researchers. Number of dives per month varied depending on sea conditions and availability of divers (range 1-6 dives per month). Generally photographs were taken on only a single dive per day, however, when time allowed, a second dive may have been conducted and photographs taken.

Dives were conducted from one of two boats (Save Our Seas shark research boat, Xiphodon, and the Shark Explorer, a commercial dive boat). The boat was set at anchor during each dive, although, due to the shallow depth of the water and the presence of rocks near the surface, the position of the boat at anchor and therefore the starting point of each dive, varied with the direction and intensity of sea swells and wind. Once at anchor, at least two divers entered the water with at least one diver equipped with a waterproof digital camera (Cameras used: Canon 7D & Sealife DC 1000). The divers swam approximately 2 m from the sea floor, following recognisable gullies that stretch across the site and ending in the starting location. Although the starting point varied, dives generally covered the entire study area. Each dive lasted between 45 - 60 min and covered an area of approximately 0.033km^2.

Many of the data were collected by a SCUBA diver conducting eco-tourism dives at the site. While attempts were made to standardize methods, the presence of tourists on the dives introduced considerable variation to the data collected, as dives were typically focused on aggregations of sharks in areas optimal for tourist viewing opportunities. This bias was considered during analysis of results (See Chapter 4.4.2).

When a shark was encountered, photographs were taken to enable individual identification (*Chapter 3.2.2*) and habitat type (*Chapter 4.2.1*). Each individual encountered was photographed both dorsally and ventrally (when possible) to allow for sexing of individuals. The diver operating the camera would approach the individual from the side and at least 1 m above the animal. When directly above, a single photograph was taken of the dorsal surface of the individual.. We attempted to photograph every individual encountered on a dive (mean: 16, range: 3 - 70), although this was not always possible. To limit the effect of human interaction on the behaviour of the sharks, care was taken not to interfere with the shark in any way, including not touching the animal, not blocking its path nor allowing the animal to become boxed in between divers or surrounding rocks.

2.2.2 – Sexing individuals:

Sex was identified by the presence or absence of claspers, which are located on the ventral side of the shark, between the pelvic fins (Figure 2.3). Original attempts to record the sex of an individual involved a second diver recording the sex of the individual on a slate as it was photographed. However, as time was not recorded with the sex information, and the second diver was not always certain when a photograph had been taken, we were unable to definitively match all sex records to the correct individual. Data on the sex of individual sharks collected using this method were thus discarded.

Sex was then instead identified from ventral photographs (Figure 2.3). Once the dorsal photograph had been taken and the individual had swum past the diver, the diver would descend and attempt a second photograph of the ventral side of the animal. An image of the diver's hand was taken in between each pair (dorsal and ventral) of photographs of a shark to enable the matching of sharks with the description of sex.

Not every shark was sexed on its first encounter. However, the more times an individual was encountered, the more likely it is that the sex of that individual will be determined on one of the sightings. An individual that was sighted more frequently was therefore more likely to be sexed than

an individual that was sighted only once. This may then lead to a bias in sex ratios towards that sex with longer residency time at the site. To control for this, the sex of the individual was only considered if it was identified on the first sighting.

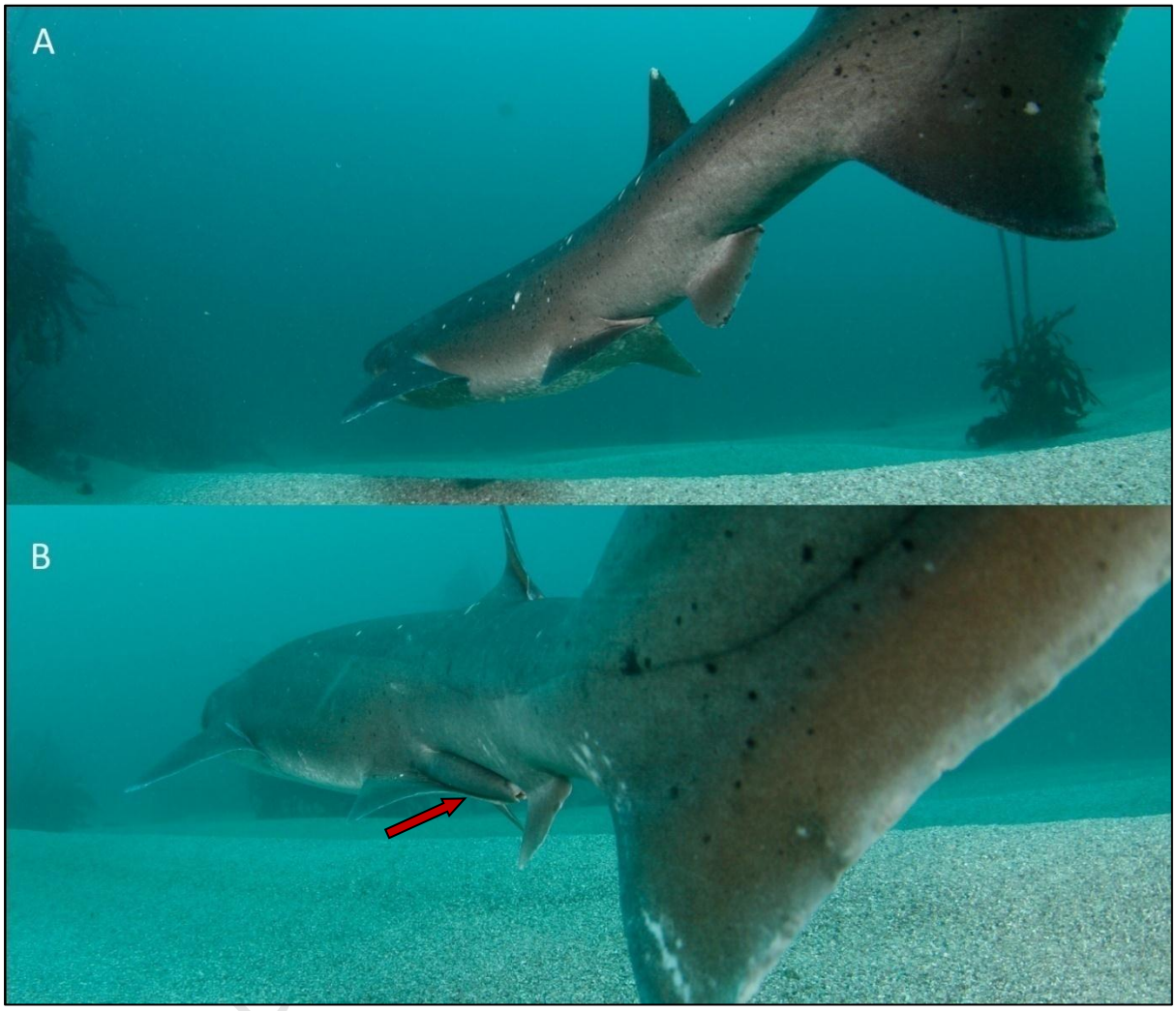


Figure 2.3: Ventral photographs of sevengill sharks swimming away from the photographer. A: Female without claspers. B: Male with claspers (red arrow).

Chapter 3 –Demographics of Sevengill Sharks, *Notorynchus cepedianus* at an aggregation site in False Bay, South Africa.

3.1 – Introduction

3.1.1 – Population demography

As human awareness of environmental issues grows and the need to understand ecosystems intensifies, there is an increasing need for further research into population demography and life histories of organisms. The assessment of shark populations can be impaired by a lack of biological information (Cortes 1998). Effective conservation of a species is best managed from a strong ecological foundation (Arzoumanian *et al*. 2005). Data on the demographics of a species are useful to determine the strength of regulation operating on a population, including elements of abundance and extinction risk (Bradshaw *et al.* 2007).

Demography is defined as the quantitative description of a population, including elements of its size, age and sex composition, as well as its spatial distribution (Krohne 2001). The study of population demographics provides a framework with which scientists may assess the health of a population. When coupled with knowledge of life history traits of a species, it is possible to determine the resilience of the population to threats it faces, including human impacts from over - exploitation. Population viability analysis (PVA), a process by which one evaluates population models to anticipate the likelihood that the population will persist through some chosen time into the future (Boyce 1992), provides a means to examine the relative contributions of different environmental factors on population change (Bradshaw *et al.* 2007).

While demographic analysis is a useful tool for assessing shark stocks and resilience, a broad range of life history information is required before one is able to fully assess the state of a population. These include age at sexual maturity, maximum age of reproduction, rate of natural mortality and natality of a specific age (Chen & Yuan 2006). Such assessments need to cover enough of the population across its entire range.

Slow growth, late age at maturity and low fecundity in many elasmobranches lead to low levels of population growth, making them vulnerable to pressures placed by fisheries and impeding the recovery of depleted populations (Camhi *et al.* 1998). Therefore, knowledge of population demographics is essential for assessing the conservation status of a species (Speed et al. 2007).

Historically, little effort has gone into research and management of elasmobranches, due to their relatively low commercial value, relative to teleost fishes (Camhi *et al.* 1998). Consequently, there has been little incentive to research, resulting in large gaps in the knowledge of life history traits of most elasmobranches.

3.1.2 – Capture-mark-recapture studies

3.1.2.1 – Conventional methods

The ability to follow the fate of individual animals over time allows scientists to estimate survival parameters of a species under natural conditions (Lebreton *et al.* 1992). Such studies can provide insight into not only survival, but also estimates of abundance, site fidelity and movements (Nichols Pollock 1983, Kohler & Turner 2000, Arzoumanian *et al.* 2005, Bradshaw *et al.* 2007). The ideal situation would be for biologists to follow all individuals in a population from birth to death, to gain a complete picture of the demographics of the population (Lebreton *et al.* 1992). However, this is impossible for most wild animal populations, therefore alternative means of following individuals in a population are required. Such alternative methods are of particular importance in the marine environment, where the opportunities to make observations of animals are limited.

Capture-mark-recapture (CMR) studies provide a means by which researchers can identify individual animals, so as to account for their survival when seen again. The basic principles of CMR are simple: a set of individuals from a population are sampled, marked for future identification and then released back into the general population. If an individual is then recaptured during subsequent sampling sessions, after having been at liberty for a period of time, and provided it can be re-identified, then these data can be used to estimate population size.

Initial objectives for most tagging studies are to investigate movements and migrations of individuals, while more recent techniques have allowed for the study of population dynamics (Kohler & Turner 2001). Marked animals have been used in population studies as far back as the 1930's (Jackson 1933, Lebreton *et al.* 1992). While the original emphasis of CMR population studies was simply to determine population size, modern modelling techniques allow one to ascertain a wealth of information from CMR data, including estimates of survival, recapture probability and migration, as well as the effect of both intrinsic (age, sex, size) and extrinsic factors (environmental conditions) on these estimates (Lebreton *et al.* 1992).

Traditionally, Capture-Mark-Recapture (CMR) methods relied on the capture and physical marking of an animal with a tag, or a marking system, that could later be identified upon recapture or re-sighting (Meekan *et al.* 2006). Conventional tags are defined as those that can be identified without the need of specialized equipment (Kohler & Turner 2001).

CMR methods have since been used on all major animal groups, including birds (Pradel *et al.* 1997, White and Burnham 1999, Schaub *et al.* 2001), mammals (Nichols & Pollock 1983, Parmenter *et al.* 1998), amphibians (Reading 2007, Phillott *et al.* 2007), reptiles (Ballinger 1973, Civantos *et al.* 1999, Bonnet *et al.* 2002) and fish (Ishii 1979, Connor *et al*. 2003, Curtis & Vincent 2006).

Tagging for CMR studies has also been used extensively on a variety of shark species, including the pacific angel-, *Squatina californica* (Cailliet *et al.* 1992), lemon- *Negaprion brevirostris* (Brown & Gruber 1988, Feldheim *et* al. 2002, Freitas *et al.* 2006), blue- *Prionace glauca* (da Silva *et al.* 2005) and raggedtooth sharks, *Carcharias taurus* (Dicken *et al*. 2007). The first tagging of elasmobranches in South African waters began in 1964, with a programme by the Oceanographic Research Institute (ORI) for the tagging of sharks in Durban (Davies & Joubert 1966).

Physical tagging, however, is an invasive method, which may be stressful and possibly harmful to the individuals being studied (Kohler & Turner 2000). Factors such as stress, discomfort and energetic costs to the individual all need to be considered when justifying the use of this

methodology. These factors need also be taken into account when drawing conclusions about an individual's behaviour when released, as stress factors can influence an individual's natural behaviour, or reduce performance (Kohler & Turner 2001, Wilson & McMahon 2006). A further drawback of conventional tagging is the loss of non-permanent tags, often referred to as 'tag shedding'. The loss of tags can reduce the number of recaptures, resulting in underestimates of survival (Dicken *et al*. 2006) and overestimates of abundance, therefore the rate of tag shedding needs to be estimated, so relevant adjustments can be made (Barrowman & Myers 1996). Dicken *et al.* (2006) found that the attachment of both dart and disk tags to *C. Taurus* also inflicted damage to the sharks. Tag-inflicted damage was exacerbated by the presence of biofouling on tags, which caused continual irritation and abrasion of the wound. As the negative effects and potential biases of invasive research become clearer, it becomes important to develop new non-invasive or minimally-invasive techniques to research wild populations.

3.1.2.2 – Photo identification

Recent developments in non-invasive mark-recapture studies include the use of photo identification (photoID) as an alternative method for individual identification. PhotoID involves the use of natural markings to identify an individual from photographs taken in the field (Speed *et al.* 2007, Dudgeon *et al.* 2008, Marshal & Pierce 2012). The use of photographs for identification eliminates the need for capture or handling of an animal, reducing the stress and discomfort on the individual and providing data that are less biased by the effects of stress. The ability of modern digital cameras to take thousands of photographs in quick succession means that researchers are not limited in the number of individuals that can be sampled. Computers also allow for the storage of large identification databases, against which new sightings can be compared, often with the aid of automated identification software.

The use of photoID is becoming a widely accepted method for mark-recapture studies (Speed *et al.* 2007, Marshall & Pierce 2012) having been tested on a broad range of species, both terrestrial and marine, including badgers, M*eles meles* (Dixon 2003), tigers, *Panthera tigris* (Karanth and

Nichols 1998), monk seals, *Monachus schauinslandi* (Harting*et al.* 2004), whales, *Eubalaena glacialis* (Fujiwara and Caswell 2001) and a variety of shark species including nurse, *Ginglymostoma cirratum* (Castro & Rosa 2005), reef, *Carcharinus melanopterus* (Porcher 2005), whale, *Rhincodon typus* (Arzoumanian *et al.* 2005, Meekan *et al.* 2006) and white sharks, *Carcharodon carcharias* (Domeier & Nasby-Lucas 2006).

Species that are suitable candidates for photoID tend to exhibit certain characteristics, namely; relatively small numbers in a population, distinctive marking present in a high proportion of the population and large overall size (Marshall 2008). Sevengill sharks fit these criteria, making them ideal candidates for PhotoID based CMR studies (Figure 3.1).

Figure 3.1: Heterogeneity in natural markings of sevengill sharks.

3.1.3 – Sex ratios and sexual segregation

Segregation of animal populations by sex has been documented in a variety of animals, with males and females living apart for much of the year, coming together only during mating (Ruckstuhl & Neuhaus 2000). These include many species of fish (Sims *et al*. 2001), birds (Ornat & Greenberg 1990), reptiles (Wearmouth & Sims 2008), and mammals (Ruckstuhl & Neuhaus 2000).

Sexual segregation has been considered a general characteristic within shark populations (Springer 1967) and has been documented in a number of species, including scalloped hammerhead, *Sphyrna lewini* (Klimley 1987), shortfin mako, *Isurus oxyrinchus* (Mucientes *et al.* 2009), grey reef, *Carcharinus amblyrhynchos* (Economakis & Lobel 1998), nurse, *Ginglymostoma cirratum* (Carrier *et al.* 2004) and white sharks *Carcharodon carcharias* (Robbins 2007).

The term sexual segregation is one which must be used with caution, as the broad term 'sexual segregation' can be divided into two classes: habitat and social segregation (Ruckstuhl & Neuhaus 2005). In terms of sexual segregation, habitat segregation describes differences in the spatial distribution of males and females and can be considered to fall in line with spatial segregation. Social segregation, on the other hand, can occur independently of habitat segregation, for example if males and females use the same habitat, but at different times (Ruckstuhl & Neuhaus 2005). For the purpose of this study, the term sexual segregation will refer to habitat/spatial segregation, unless otherwise stated. Sexual segregation at a particular site may be evident in sex ratios of individuals at the site. A skewed sex ratio can be considered a sign of partial sexual segregation. However, care must be taken in this interpretation, for if the ratios are skewed across the entire population, it may not be a result of sexual segregation, but rather an artefact of differing ratios at birth or different survival between sexes.

Some evidence exists for sexual segregation in sevengill sharks. Sexual segregation in sevengill sharks in Argentina was examined by Lucifora *et al.* (2005), who found that the sex ratio of juveniles could not be significantly differentiated from 1:1. The sex ratio of adults could not be tested

statistically due to small sample sizes, however, seasonal changes in the sex ratio of adults were observed, with only males found in December, only females found from January to March and both sexes found in April, suggesting spatial segregation in adults. Barnett *et al.* (2010c) found sex ratios of sevengill sharks in Tasmania to be biased towards females, displaying a ratio of 2.7:1, while Williams *et al.* (2011) observed that the sex ratios of sevengill sharks on the Pacific Northwest coast were biased towards males, suggesting some level of sexual segregation in the species.

3.1.4 – Demographics of sevengill sharks

Despite their widespread distribution, and their potential importance in coastal ecosystems as apex predators, the population status of sevengill sharks remains largely unknown. Much of the literature on sevengill sharks focuses on diet (Ebert 1989, 1991b, 2002, Lucifora *et al.* 2005, Barnett *et al.* 2010b), growth (Ebert 1989, 1996, Van Dykhuizen & Mollet 1992, Braccini *et al.* 2010) and age at sexual maturity (Ebert 1989, 1996, Van Dykhuizen & Mollet 1992, Lucifora *et al.* 2005). More recently, attention has been paid to movement patterns and site fidelity of individuals (Barnett *et al.* 2010c, 2011). Population structure of sevengill shark populations has been investigated in coastal areas of California, Patagonia, Tasmania and Washington State (Ebert 1989, Lucifora *et al.* 2005, Barnett *et al.* 2010a, Williams *et al.* 2012). While these studies all provide valuable insight, much research is still required before we can fully understand the life-history and resilience of the species towards human impacts. There are currently no published data on the survival of the species, resulting in a major gap in our ability to understand the effects of human activities and other natural effects on populations of sevengill sharks.

3.1.5 – Aims

The aims of this chapter were to provide survival and sex-ratio estimates for sevengill sharks that aggregate in a protected area. It is hoped that the data will aid in future analysis of population demographics of the species within South African waters. I used a photoID database of the sharks to estimate recapture probabilities and apparent survival. Survival was assessed between sexes and

over seasons and years. I also investigated sex-structure, as a potential indicator of sexual segregation at the site.

3.2 – Methods

3.2.1 – Data collection

Methods for data collection are described in Chapter 2.2.1.

3.2.2 – Individual identification:

A non-invasive method for identification was implemented using PhotoID. The use of computer programs for identification are constrained by the angle at which the image is taken, decreasing in accuracy as you increase the angle of incidence of the image. Identification of individuals was subsequently done by eye, to maximise the number of images suitable for identification. This method uses a range of physical attributes to differentiate between individuals. For sevengill sharks, the dorsal surface of the shark was used for identification, as this displayed the most prominent attributes for identification (Figure3.2).

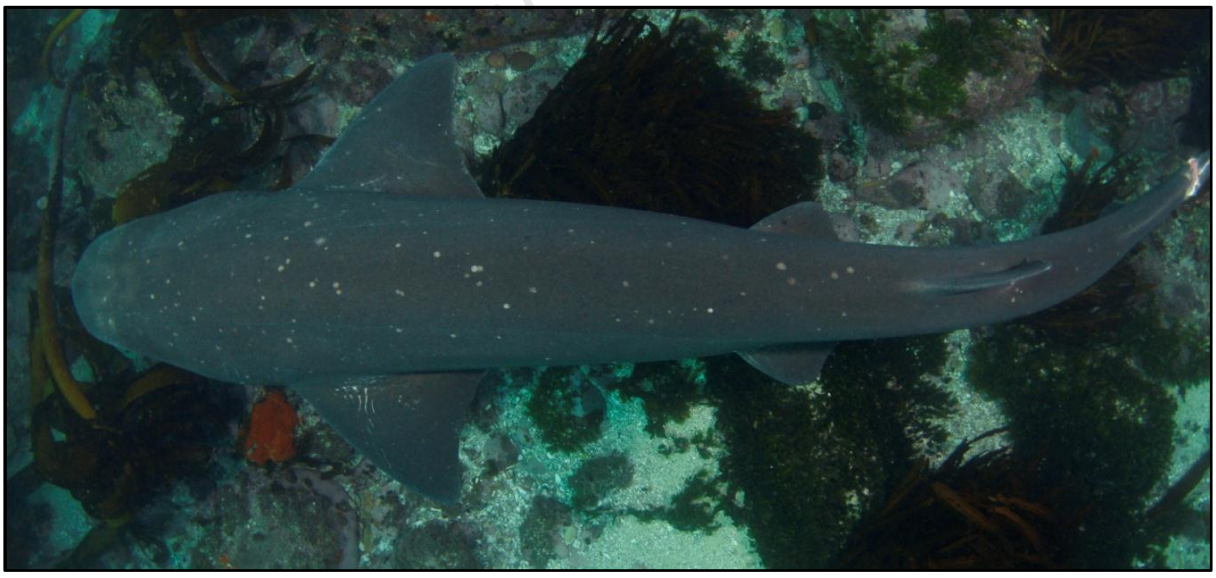


Figure 3.2: Example of photograph for identification of a sevengill shark.

3.2.2.1 – Identification attibutes

A set of characteristic markings were used to compare photographed individuals to one another and to identify sharks to the level of individual. As each attribute has its drawbacks, no single attribute was used alone to identify an individual. Therefore a combination of multiple attributes was used to improve the confidence of accurate identification. These attributes included:

Black spots: The dorsal surface of the shark is covered in black spots. These spots can vary in number and size from individual to individual. The black spots are permanent and considered to be unchanging over time (Smale, pers. com.), providing a unique marking for individual identification. However, the spots can be difficult to discern, especially when the image lacks contrast. Furthermore, dark spots are often either rare or too dense, limiting their use as a reliable means of identification.

White spots: Clearly visible on the dorsal surface of the sharks and are the most easily identifiableexternal marking for the species. As with the black spots, the white spots can vary in both size, number and distribution amongst individuals (Figure 3.1). Although the diversity and visibility of the white spots make them seemingly ideal identifying attributes, they are constrained by the fact that they are not genetically based but rather caused by a fungus (Ebert pers. com.), and hense are subject through the individuals lifetime.

Wounds/scars: Scars on the pectoral fins, as well as on the sides of the body, can also be used as a means of discerning individual sharks. Wounds/scars can vary from small scratches to severe deformations of the fin. Scars, however, are extremely variable over time, with fresh wounds forming new scars and old scars becoming less defined as they heal. This is a major drawback for the use of scars for identification, although some severe scarring can be used as a long term identifying mark. While the presence of a common scar on two images can be used to make a positive identification between the two images, the absence of the scar on one image cannot completely discount it from being a match to an image that does display a scar.

Fin notches: Like scars, fin notches on the trailing edge of the pectoral fins can be used as supporting attributes for identification (Figure 3.3). Again, consideration must be taken for changes in the fin notches over time.

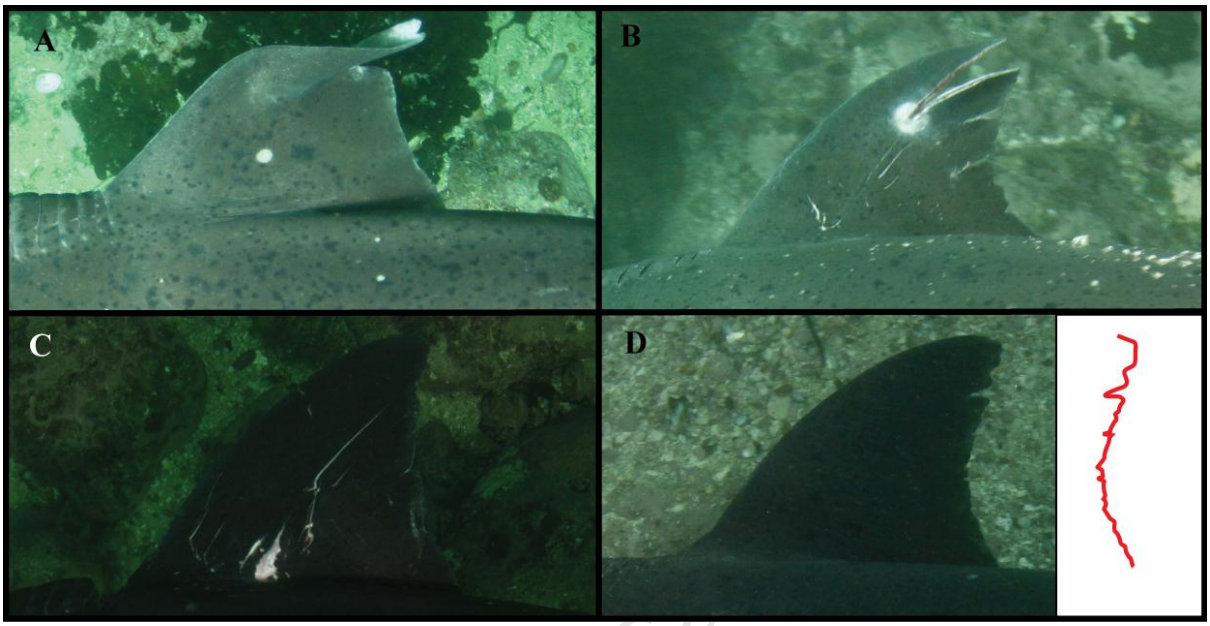


Figure 3.3: Scaring and fin notches on the pectoral fin of sevengill sharks. A: Severe deformation of the pectoral fin. B: Severe cut and minor scaring. C: Severe scaring. D: No Scaring, displaying fin notches (inset: contour of pectoral fin trailing edge, used for ID purposes).

3.2.2.2 – Identification protocol

Each new image was opened in an image viewing program (Nikon View NX 2), rotated to a left facing orientation, cropped and adjusted for brightness and contrast if required, producing a sample image (Figure 3.3 above).

The sample image was then given a label based on four quickly observable criteria, coupled with a sequential three digit number:

1. Sex: Male, Female or Unknown, given the codes M, F, U respectively, based on the corresponding ventral image.
2. Pectoral Scarring: Neither, Left, Right or Both (N, L, R, B), depending on whether scars were present on either of the pectoral fins.
3. Severity of scarring: Minor, Severe or None (M, S, N).

4. Body Scarring: Simple presence or absence of scarring on the body, given codes P and A respectively.

Using these codes, a female individual, with minor scarring on the left pectoral and no scarring on the body would be labelled FLMA001, with the number referring to the reference number for that individual. This code, while not providing definitive search criteria, gives some indication of where in the database to begin the search, to allow maximum likelihood of finding a match with minimal effort. If an individual showed minor scarring on the left fin, the search could begin with other individuals with similar scarring, reducing the time taken for identifications. Sex was considered the only absolute defining characteristic, therefore females need not be compared to males and vice versa, but all individuals need to be compared to individuals of unknown sex. Individuals with no scarring need not be compared to individuals with severe scarring, although consideration must be taken for possible healing of scars and the addition of new scars. An individual was only considered to have no scarring if the body appeared in perfect condition, with no signs of scarring, including lighter or darker areas on the surface from healed scars.

Once the image had been adjusted and labelled, it could be run through the database of known individuals to determine whether the shark was a new individual, or a resighting of a previously identified individual.

Procedure for identification:

Three stages of identification were carried out, each producing an identification database consisting of a single reference image for each individual:

1. Single Session: All images from a single sampling session (one day of diving) were compared and individually labelled to determine the number of individuals encountered during that sampling session.
2. Six-Month Groupings: Single session data were compared to identify all the individuals observed within a six month interval (January – June and June – December of each year).

This produced a database of the total number of individually recognisable sharks at the study site in a six month period.

3. Overall Grouping: Sample images from each of the six month interval datasets were compared to reference images in the complete database to get an overall sighting regime, with a single sample image for each individual.

As the database increased, the time taken to make an identification increased, therefore by breaking the identifications into smaller groupings, only one sample image of any single individual was run through the full database, decreasing the time required for identification.

Single session data: The first image from the session was labelled as shark ****001 (using the labelling criteria listed above) and placed in the relevant identification database for that session. Each new image was then compared to each image in the identification database using the identification attributes listed above. A match was considered to be made when at least two of the four criteria were met (excluding minor scars and notches). If a match was made, the new image would be labelled with the same code as the reference image. If the new image was of better quality than the reference image, the reference image would be replaced by the new image, else the original image would be kept and the new image would not be added to the reference database. Should no match be made, the image was considered a new individual and added to the identification database, labelled using the above mentioned criteria and given the next sequential number in the identification database. This procedure was repeated until all new images had been run through the identification database, which by the end would contain a single reference image for each individual encountered during that session.

Six-month grouping data: The identification database from the first single-sampling session in the period would be duplicated to form the basis of the identification database for the six-month period. The same identification procedure was then followed for each image in each of the identification databases, with each image either being identified as a resighting, or as a new individual, and labelled accordingly. As each image was identified and relabelled, the original

unrefined images for each day were also relabelled so that the numbering of the raw data matched with that of the refined databases.

Overall grouping data: The same procedure was followed as for the six-month grouping data, except the six-month identification databases were used instead of the single session identification databases. The number with which the reference image was labelled in this final database was used to produce a unique code for each individual, by which each individual could be referred.

Once the overall database was completed, all images would have then been identified and each individual sighting from each sampling session had the relevant code for that individual.

3.2.3 – Statistical analyses

3.2.3.1 – General analyses

The numbers of observations were compared between all four seasons using one-way ANOVA in Statistica 10 (StatSoft Inc.). Observation frequency data did not meet assumptions of normality, and were therefore log transformed, resulting in normalised data. Data from all years were pooled for analysis, incorporating two Springs, three Summers, two Autumns and two Winters.

3.2.3.2– Capture-mark-recapture

Capture-mark-recapture (CMR) methods were used to estimate survival and population size (Lebreton *et al.* 1992) using the program MARK 6.1 (White & Burnham 1999). Data were analysed using Cormack-Jolly-Seber (CJS) models.

The underlying assumptions for CJS models are:

-Homogeneity in capture probability – Every animal in the population at time (i) has the same probability of being captured (p_i)

-Homogeneity of survival – Every animal in the population has the same probability of surviving immediately after time i.

-No tag loss

-No misidentification

-All captures instantaneous relative to interval between sampling periods and each release made immediately after capture.

The general model, including all effects of time and sex, was tested for goodness of fit (GoF) using the Program RELEASE in Program MARK and Program U-CARE. Standard procedures for model fitting and notation were used, with Akaike's Information Criterion (AIC) being used for the basis of model selection (Lebreton *et al.* 1992).

Two sets of models were run, set according to the grouping of sampling sessions.

1. Data grouped by month
2. Data grouped by season (three month groupings)

Seasons were defined as:

- Spring – September, October, November
- Summer – December, January, February
- Autumn – March, April, May
- Winter – June, July, August

As GoF testing in U-CARE revealed high levels of transience in females of the population, models were altered using age-effect analysis, separating parameters for initial observations from all subsequent observations. Models were also constrained using the design matrix dependant on if they were caught at the previous sampling session to account for a trap-dependence detected by GoF testing. To maintain consistency, constraints were applied to all three groupings: female, male and unknown sex.

3.2.3.3 – Sex Structure

Data on the sex structure of the population were analysed using chi-squared analysis in Statistica 10 (StatSoft Inc.). Only individuals for which sex was identified on first encounter were considered in this analysis.

3.3 – Results

3.3.1 – General results

A total of 68 dives were carried out between 2009 and 2011, during which 1119 photographs were taken. Sevengill sharks were observed on all 68 occasions, with a minimum of three and a maximum of 70 individuals sighted on a single dive. An average of 16.45 (SD = 11.39) sharks were photographed per dive. Individuals were successfully identified using natural markings and their markings showed little change over the time frame of the study (Figure 3.4). Additional white spots were observed on some individuals, although these spots usually appeared smaller and fainter than older spots, allowing for original patterns to still be observed. No changes in black spots were observed.

From these 1119 observations, 587 individuals were identified using PhotoID techniques, of which 224 were observed more than once, a total recapture rate of 38.2% (Figure 3.5). Over 12% were observed on at least four occasions and over 7% were observed over five occasions. Two individuals were observed a total of 12 times each. The longest time at liberty between observations of a single individual with no observations between was 754 days, while the longest period between first and last observation of a single individual was 825 days.

The discovery curve representing new individuals observed over sampling effort (Figure 3.6) shows a strong linear trend (R^2 = 0.993), with little change in discovery rate over time. No plateau was reached, nor was there any sign that discovery rate was slowing to meet a plateau, suggesting that the entire population was not sampled, but rather a steady stream of visitors to a specific site.

No significant difference was found in the number of unique individuals observed between seasons (Figure 3.7, ANOVA $F_{3,58}$= 1.6274, p = 0.1929).

Figure 3.4: Top image shows individual SGS041 on first sighting, bottom image shows individual SGS041 on last sighting after 825 days at liberty.

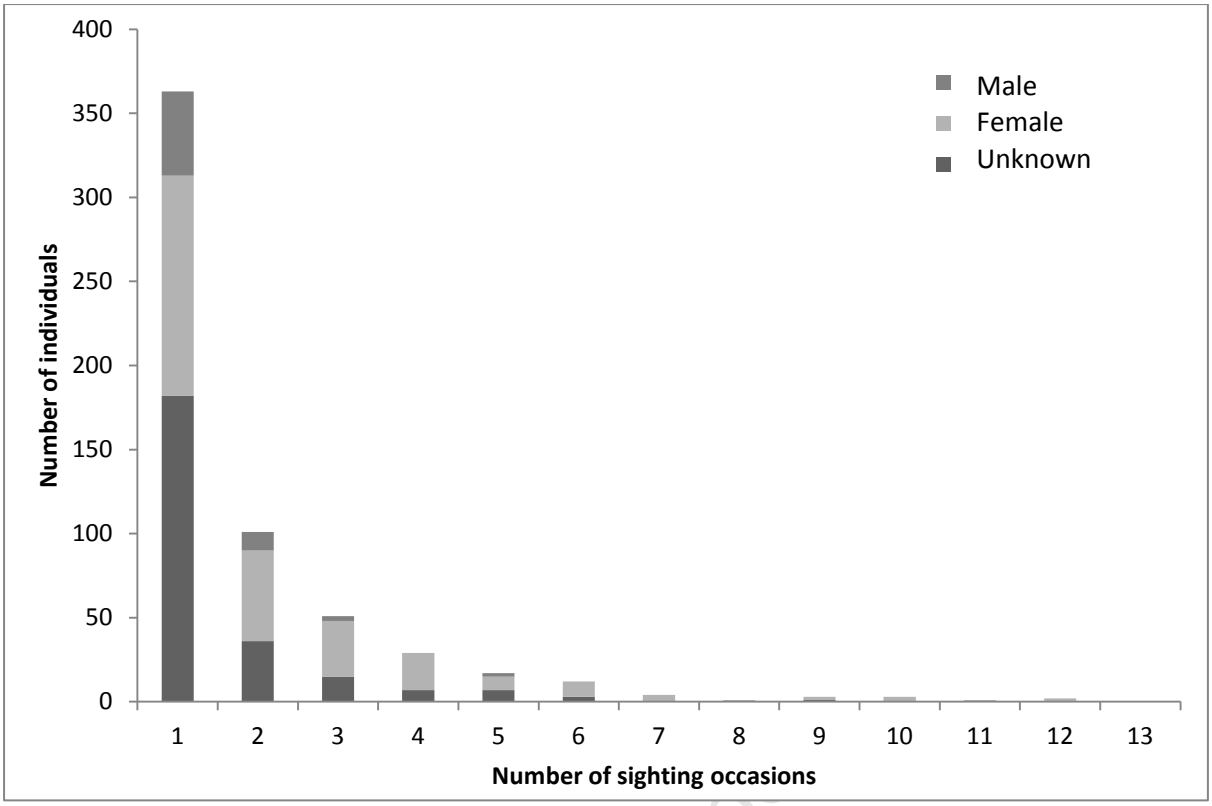


Figure 3.5: Total number of male, female and unknown sex individuals resighted during the study period.

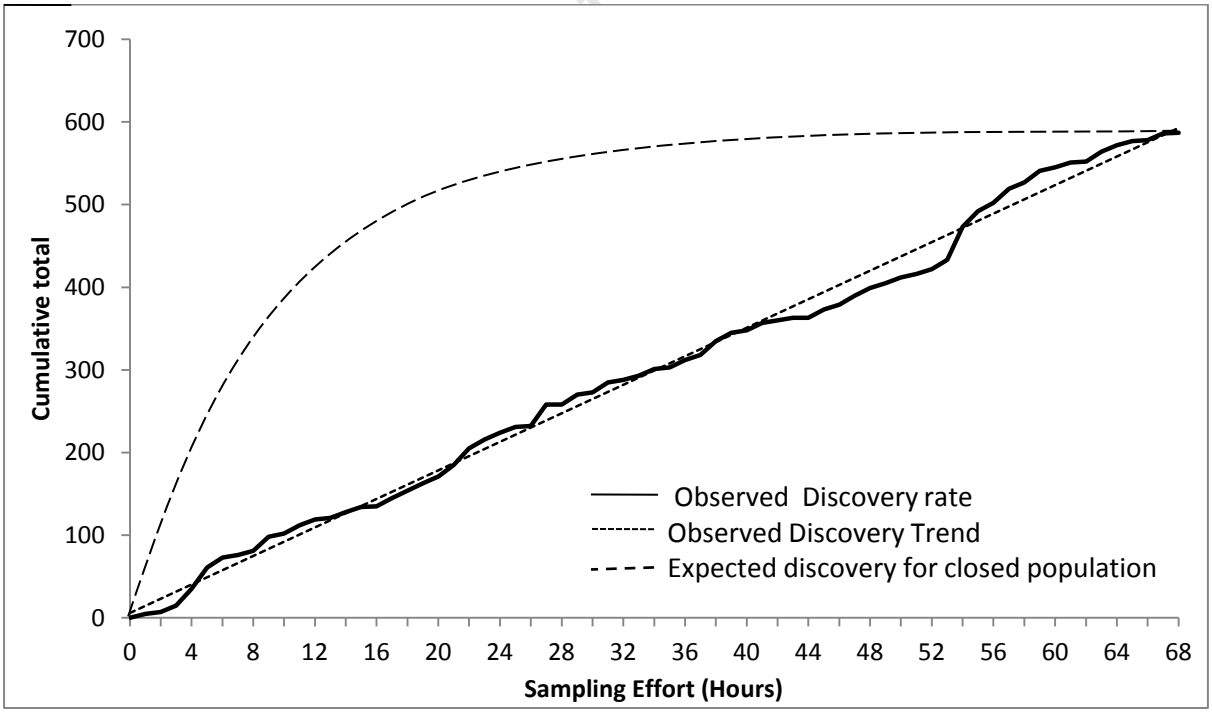


Figure 3.6: Discovery curve for sevengill sharks, showing cumulative totals of the number of individuals identified plotted against units of effort (taken as an average of one hour per sampling session). The upper curve shows an expected discovery curve for a closed population, in which all individuals have been sampled.

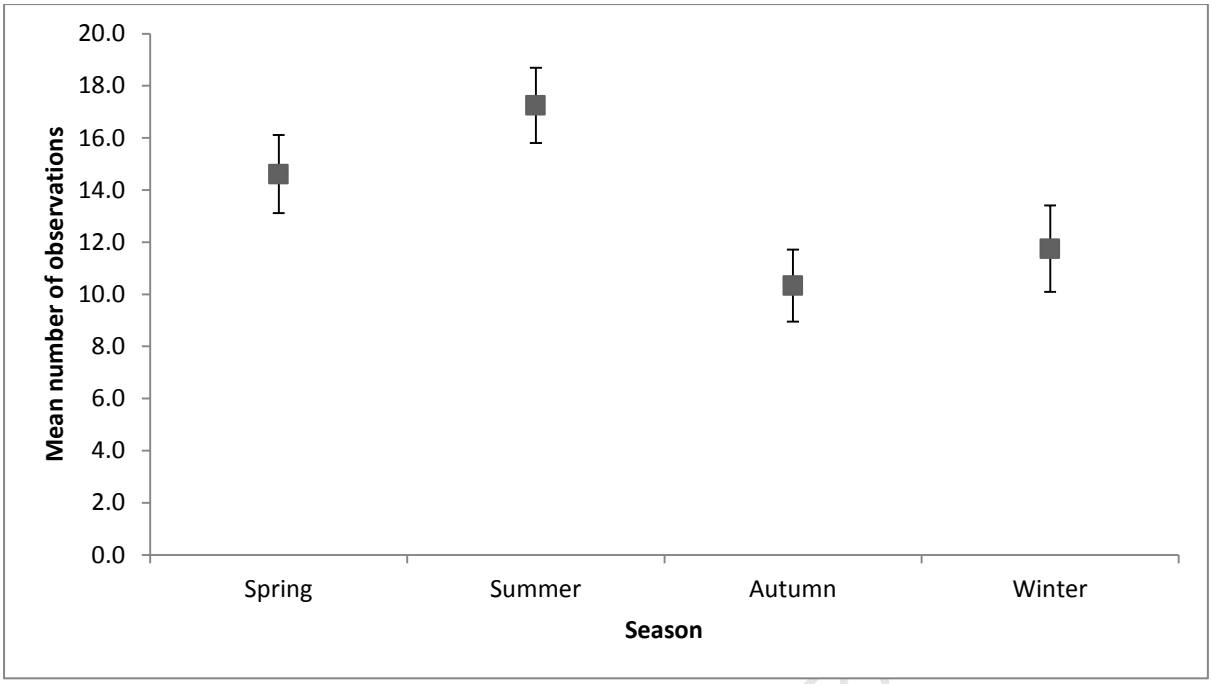


Figure 3.7: Mean number of observations per sampling session over all four seasons. Vertical bars denote 95% confidence intervals depicting variation within each season.

3.3.2 – Sex structure

Data on the sex of individuals were collected for 336 individuals, of which 66 were male and 251 were female. The remaining 251 individuals (42.75%) were of unknown sex.

The sex ratio observed for the population as a whole differed significantly from an expected ratio of 1:1 (χ^2 = 123.857, *df* = 1, p<0.0001). The null hypothesis of an equal sex ratio in the population was therefore rejected, and the alternative hypothesis of an unequal sex ratio accepted. The observed sex ratio (males : females) for sevengill sharks was approximately 1:4.1.

Seasonally, sex ratios differed from an expected ratio of 1:1 for all four seasons (Figure 3.8, Spring: χ^2 = 76.2222, *df* = 1, p<0.0001; Summer: χ^2 = 88.0434, *df* = 1, p<0.0001; Autumn: χ^2 = 62.2631, *df* = 1, p<0.0001; Winter: χ^2 = 40.1636, *df* = 1, p<0.0001), with all four seasons skewed towards females.

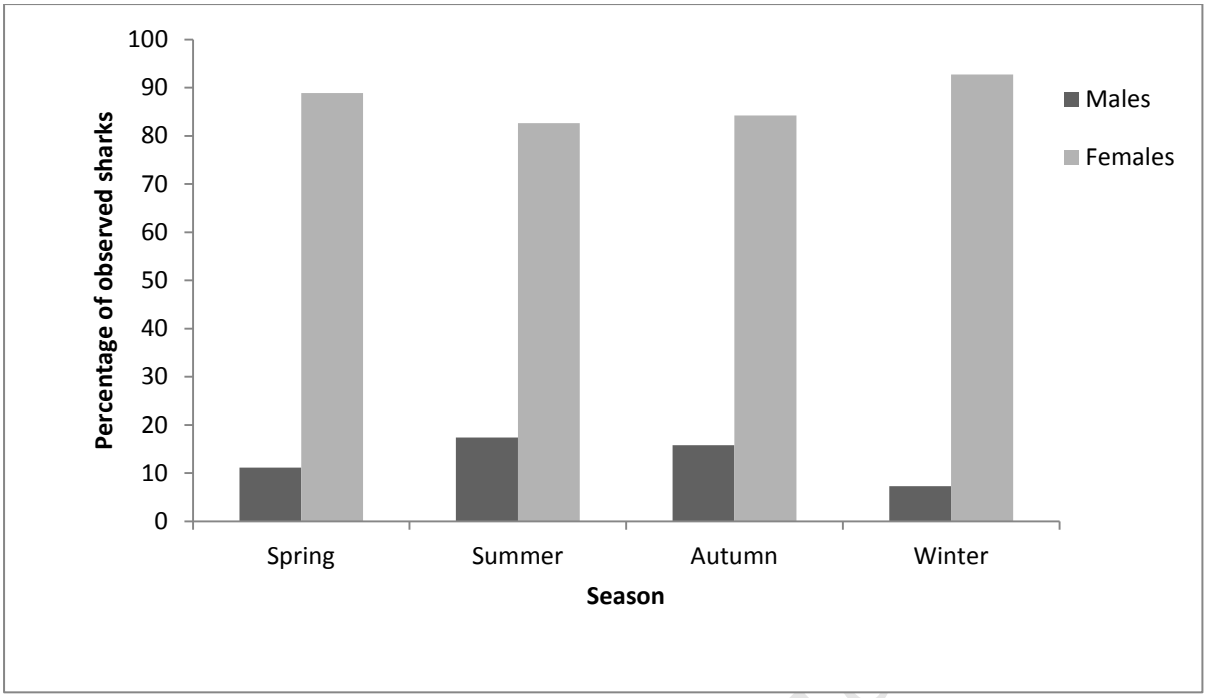


Figure 3.8: Percentage of males and females observed at the aggregation site during each season.

3.3.3 – Survival

3.3.2.1 – Monthly grouped data

A total of 24 'capture' sessions, grouped into monthly datasets, were used in initial models. A fully time-dependant model incorporating sex {Phi(t.s)p(t.s)} was used as the general model, incorporating 127 parameters, where Phi represents the parameters for survival and p represents the parameters for recaptures.

Goodness of fit (GOF):

Combined results from GOF Test 2 and Test 3 (Program U-CARE) show that the general model {Phi(t.s) p(t.s)} does not differ significantly from assumptions underlying the model (χ^2 = 142.168, *df* = 146, p>0.05), suggesting that the general model adequately fits the data. Inspection of individual elements of the GOF tests in Program U-CARE showed evidence for females to fail GOF for Test3.SR (χ^2 = 25.1167, *df* = 15, p<0.05) and Test2.CT (χ^2 = 42.3312, *df* = 20, p<0.05), suggesting heterogeneity in recapture probabilities. Females displayed a high level of transience (Transience Statistic = 3.355,

P<0.005) and 'trap-happiness' (Trap Dependence = -4.1447, p < 0.005). These discrepancies were accounted for in the model design matrix.

Initial model selection (Table 3.1) did not account for transience and trap happiness in females. These models suggested survival to be determined by sex and for recapture probabilities to vary over time.

Table 3.1 – Summery of model selection for unconstrained Cormack-Jolly-Seber models on monthly grouped data of Sevengill sharks. Models consist of two components, Survival (Phi) and recapture probability (p). Model selection was based on quasi-likelihood Akaike's Information Criterion (QAICc). *K* is the number of estimated parameters. The top five ranked models are shown. The models are named according to standard conventions, where (s) show sex dependence, (t) shows time dependence and (.) represents constant time and no sex dependence.

Model		ΔQAICc	QAICc Weights	*K*	Deviance
1	{Phi(s) p(t)}	0	0.56423	26	1302.004
2	{Phi(s) p(t.s)}	0.5237	0.43424	72	1200.433
3	{Phi(.) p(t.s)}	11.8213	0.00153	70	1216.384
4	{Phi(t) p(t.s)}	44.6605	0	91	1199.321
5	{Phi(t.s) p(t)}	62.7087	0	89	1222.223

Survival probability for the unconstrained models was divided into three categories – females, males and unknown sex. Survival probabilities for females could not be estimated, as they failed GoF tests for transience and trap-dependence. The survival for males was estimated at 0.981 (SE = 0.015, CI_{lower} = 0.907, CI_{upper} = 0.996) and the survival probability of unknown individuals was estimated at 0.777 (SE = 0.019, CI_{lower} = 0.737, CI_{upper} = 0.812).

Table 3.2– Summery of model selection for constrained Cormack-Jolly-Seber models on monthly grouped data of Sevengill sharks. Models consist of two components, Survival (Phi) and recapture probability (p). Model selection was based on quasi-likelihood Akaike's Information Criterion (QAICc). *K* is the number of estimated parameters. Models are named according to standard conventions, where (s) show sex dependence, (t) shows time dependence and (.) represents constant time and no sex dependence. Constraints for transience (trans) and trap happiness (trap) are also shown.

Model		Δ QAICc	QAICc Weights	K	Deviance
1	{Phi(trans) p(trap.t)}	0	0.999	26	2432.5204
2	{Phi(trans.t) p(trap.t)}	14.2908	0	68	2511.0377
3	{Phi(trans.t) p(.)}	73.5034	0	26	2584.541
4	{Phi(trans) p(.)}	2329.2756	0	2	2751.1548

Results for the constrained models incorporating effects of transience (trans) and trap-dependence (trap) on survival and recapture respectively are shown in Table 3.2. Due to the relatively low sample sizes in regards to sex dependent data, the effect of sex was omitted from analysis of constrained models. Model selection using QAICc values suggested the best fitting model was the fully time dependent Model 1 (Table 3.2).

Parameter estimates from Model 1 for survival were divided into two groupings: the first estimate, parameter Phi1, represents survival of transients, while the second estimate, parameter Phi2, represents animals sighted on multiple occasions. Survival probability for Phi1 was estimated at 0.742 (SE = 0.042, CI_{lower} = 0.652, CI_{upper} = 0.815). Survival of Phi2 was estimated at 0.970 (SE = 0.008, CI_{lower} = 0.950, CI_{upper} = 0.983). Recapture probabilities varied over time (Figure 3.9), ranging between 0.022 (SE = 0.011, CI_{lower} = 0.008, CI_{upper} = 0.060) and 0.506 (SE = 0.158, CI_{lower} = 0.228, CI_{upper} = 0.780).

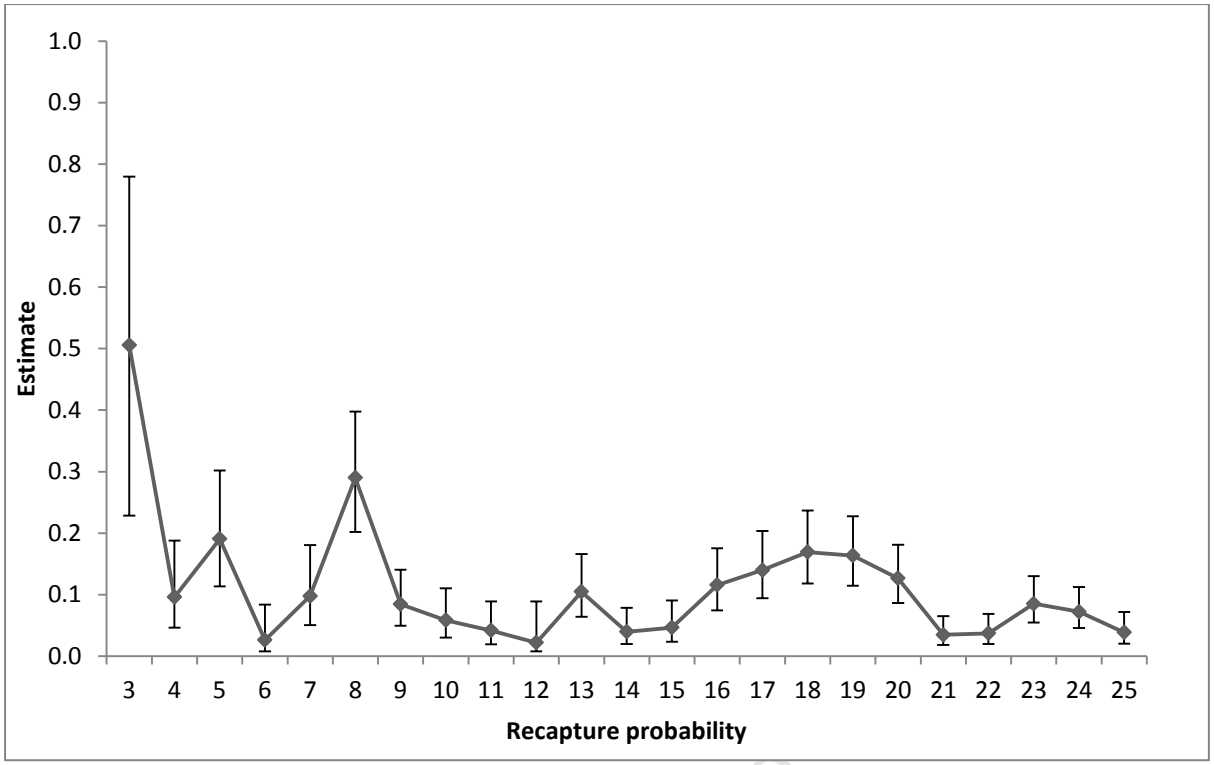


Figure 3.9: Estimates of recapture probabilities of sevengill sharks for a time dependent model for monthly grouped data. Each parameter represents an interval between two sampling sessions. Errors bars show upper and lower confidence intervals.

3.3.2.2 – Seasonally Grouped Data

A total of 10 'capture' sessions, grouped into three month seasonal datasets, were used in CJS models. A fully time-dependant model incorporating sex {Phi(t.s)p(t.s)} was used as the general model, incorporating 49 parameters.

Goodness of fit (GOF):

Combined results from GOF Test 2 and Test 3 (Program U-CARE) show that the general model {Phi(t.s) p(t.s)} does not differ significantly from assumptions underlying the model (χ^2 = 48.206, *df* = 55, p > 0.05) suggesting that the general model adequately fits the data. Inspection of individual elements of the GOF tests in Program U-CARE showed females to have a high level of transience (Transience Statistic = 2.394, P<0.01) and 'trap-happiness' (Trap Dependence = -2.25, p < 0.05). These discrepancies were accounted for in the model design matrix.

Initial model selection (Table 3.3) did not account for transience and trap happiness in females. These models suggested survival to be determined by sex and for recapture probabilities to vary over time and between sexes.

Table 3.3– Summery of model selection for unconstrained Cormack-Jolly-Seber models on three month seasonally grouped data of Sevengill sharks. Models consist of two components, Survival (Phi) and recapture probability (p). Model selection was based on quasi-likelihood Akaike's Information Criterion (QAICc). *K* is the number of estimated parameters. The top five ranked models are shown. Models are named according to standard conventions, where (s) show sex dependence, (t) shows time dependence and (.) represents constant time and no sex dependence.

Model		ΔQAICc	QAICc Weights	*K*	Deviance
1	{Phi(s)p(t.s)}	0	0.73493	30	432.0849
2	{Phi(.)p(t.s)}	2.0933	0.25804	28	438.4617
3	{Phi(t)p(t.s)}	9.2989	0.00703	35	430.5859
4	{Phi(t.s)p(t.s)}	25.93	0	49	416.2885
5	{Phi(t.s)p(t)}	44.5295	0	35	465.8165

Model selection was unable to significantly differentiate between Model 1 and Model 2 based on QAICc values (ΔQAICc = 2.0933). However, as Model 2 has a fewer parameter than Model 1, Model 2 was taken as the most parsimonious model for the data. Again, due to females failing GoF tests for transience and trap-dependence, survival estimates could not be calculated from these models.

Table 3.4– Summery of model selection for constrained Cormack-Jolly-Seber models on three month seasonally grouped data of Sevengill sharks. Models consist of two components, Survival (Phi) and recapture probability (p). Model selection was based on quasi-likelihood Akaike's Information Criterion (QAICc). *K* is the number of estimated parameters. Models are named according to standard conventions, where (s) show sex dependence, (t) shows time dependence and (.) represents constant time and no sex dependence. Constraints for transience (trans) and trap happiness (trap) are also shown.

Model		ΔQAICc	QAICc Weights	K	Deviance
1	{Phi(trans.t) p(trap.t)	0	0.9874	26	1822.298
2	{Phi(trans) p(trap.t)	8.7288	0.0125	11	1862.373
3	{Phi(trans.t) p(.)}	61.0726	0	18	1900.225
4	{Phi(trans) p(.)}	177.2551	0	3	2047.177

Results for the constrained models incorporating effects of transience (trans) and trap-dependence (trap) on survival and recapture respectively for seasonally grouped data are shown in Table 3.4. As with the month grouped data above, the effect of sex was omitted from analysis of constrained models due to small sample size. Model rankings were the same for seasonal data (Table 3.4) as they were for monthly grouped data (Table 3.2). A fully time-dependent model (Model 1, Table 3.4) was ranked the highest using QAICc model selection criteria.

However, as with the monthly grouped data, the age effect constraint applied to survival resulted in an unusually high number of parameters for time dependent survival. With the relatively small sample sizes of this study, the high number of survival parameters resulted in unrealistic estimates for survival. Model 2, which did not include a time effect on survival, was therefore taken as the best model for the data.

Parameter estimates from Model 2 for survival were divided into two groupings: the first estimate, parameter Phi1, represents survival of transients, while the second estimate, parameter Phi2, represents animals sighted on multiple occasions. Survival probability for Phi1 was estimated at 0.596 (SE = 0.046, CI_{lower} = 0.503, CI_{upper} = 0.681). Survival of Phi2 was estimated at 0.961 (SE = 0.031, CI_{lower} = 0.830, CI_{upper} = 0.991). These show that transient individuals are having a profound effect on survival estimates, evident from the difference between estimates of transience and individuals sighted on multiple occasions. Recapture probabilities varied over time (Figure 3.10), ranging between 0.033 (SE = 0.010, CI_{lower} = 0.017, CI_{upper} = 0.061) and 0.742 (SE = 0.141, CI_{lower} = 0.402, CI_{upper} = 0.925).

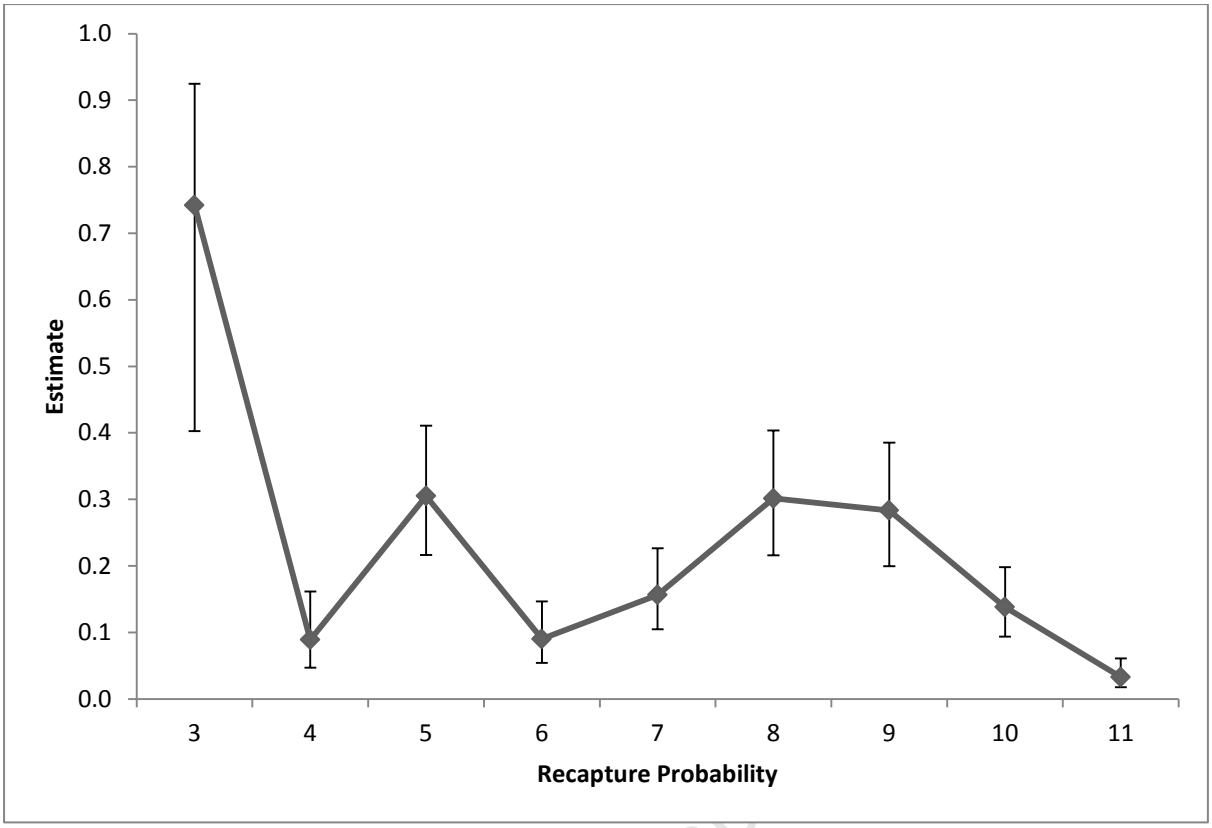


Figure 3.10: Estimates of recapture probabilities of sevengill sharks for a time dependent model for seasonal data. Each parameter represents an interval between two seasons. Errors bars show upper and lower confidence intervals.

3.3.2.2 – General survival and recapture

The survival estimates for initial observations, accounting for transients, were much lower (monthly: 74%, seasonal: 59%) than the survival estimates for individuals that were resighted (monthly: 97%, seasonal: 96%). Seasonal survival for transients was lower (59%) than monthly survival (74%). Monthly survival was relatively high at 97%, and similar to seasonal survival estimate at 96%.

Recapture probabilities were found to differ over time for both monthly and seasonal models. While no obvious trend was observed in recapture probabilities, there do appear to be slightly higher recapture rates predicted for parameters that represent intervals during spring and summer (e.g. recapture probabilities 5, 8 & 9, Figure 3.10) than during autumn and winter intervals (e.g. recapture probabilities 6, 7, 10 & 11, Figure 3.10). Similar patterns were observed in monthly grouped data, with higher values generally estimated during summer (e.g. recapture probabilities 8, 18, 19 & 20,

Figure 3.9), with lows being observed during autumn and winter periods (e.g. recapture probabilities 6, 11, 12 & 22, Figure 3.9).

3.4 – Discussion

3.4.1 – Population structure

Over the course of this study 587 individual sevengill sharks were successfully identified using PhotoID techniques at the Pyramid Rock aggregation site.

While the models used for this study do not include estimates of total population size, the discovery curve of a study can give some indications of super-population size in relation to the population observed at the site. The discovery curve for this study (Figure 3.6) shows no sign of reaching a plateau, maintaining a linear trend throughout. This suggests the super-population to be far larger than the number of individuals observed during this study. This may be linked to a high level of transience in the population, with many individuals from the population only spending a short period at the site, and not returning within the time frame of this study. The strong fit of the discovery curve to a linear trend line suggests that the arrival of new individuals into the area is fairly constant, with little seasonal variation. While the overall trend was for transient individuals using the site for short periods before moving on, there was some evidence for fidelity over longer periods. Individuals were observed to return to the site after prolonged absence (up to 754 days), showing repeat use of the site. Long-term repeat use of the site may be linked to the reproductive cycle of the species. Females were observed to return to the site after being at liberty for periods of approximately two years, which coincides with the two year reproductive cycle proposed by Ebert (1996). The lack of juveniles observed suggests that the site is not being used as a pupping ground, but it is possible that the area is used for copulation. If females do indeed have a two-year reproductive cycle as proposed by Ebert (1996), then one may predict the return of females to the site after this period of time to possibly be linked to this reproductive cycle. Anecdotal observations

of possible pre-copulatory behaviour (males swimming above females, rubbing against them) have been observed at the site (Kock, pers.com.).

Previous studies on sevengill sharks have suggested strong seasonality in shark abundances at particular sites, including North Patagonia in Argentina (Luciflora *et al.* 2005), Pacific Northwest coastal estuaries (Williams *et al.* 2011) and south-east Tasmania (Barnett *et al.* 2010c). However, no significant seasonality was observed in the abundances of sevengill sharks in the area during this study. Sevengill sharks were observed year round, with observations being made on all 68 sampling occasions. However, although not statistically significant, some differences in the number of individuals were observed between seasons (Figure 3.7). The mean number of observations per dive was highest during summer. Furthermore, local eco-tourism charters, who have dived the site frequently over a number of years, report that sevengill sharks are more abundant at the site during summer than winter. Higher abundance of sevengill sharks in summer has also been observed elsewhere in the world, including Tasmania (Barnett *et al.* 2010c) and Argentina (Luciflora *et al.* 2005).

There was a strong sex bias in sevengill sharks at the Pyramid Rock site, with females outnumbering males 4.1 to 1 over the study period. Previous observations of adult sevengill sharks have shown a level of sexual bias in the population, with biases towards both males (Williams *et al.* 2011) and females (Barnett *et al.* 2010c).

While a number of theories exist as to why sharks segregate by sex, often dealing with reproduction or growth, the reason for sexual segregation in many cases is unknown (Barnett *et al.* 2010c). In relation to the dominance of females observed in coastal areas of Tasmania in winter and spring, Barnett *et al.* (2010c) suggest that the bias could indicate that females use the inshore areas more frequently than males, staying for longer periods. This theory fits well with results found in the current study, where males were generally observed less frequently than females, and appeared to stay for shorter periods (Chapter 4). The sexual segregation observed in this aggregation in the

current study is likely linked to different uses of shallower areas in the Bay between males and females, with females spending more time in the inshore areas. The reason for females using the Pyramid Rock site more than males remains unclear. In the study by Barnett *et al.* (2010c), they suggest that the increased use of the inshore area sampled for their study is due to more than just reproduction.

3.4.2– Survival and recapture probabilities

This study has provided the first estimates of survival for the fairly poorly studied sevengill shark. These values can be used to help predict long-term trends in the populations of these sharks. The most parsimonious models for the data examined in this study supported time-based differences in recapture probabilities. While the QAICc selection criteria suggested support for time dependent survival, constraints placed on the data to account for transience (discussed in more detail below) increased the number of parameters estimated by the models. The increased number of parameters resulted in a high number of parameters which could not be estimated. Thus, models independent of time for survival were selected. Support for this decision was added by initial models that did not account for transience, which showed survival as being independent of time in all of the top three models. Transient models also excluded dependence on sex, due to low sample sizes of individuals for which sex had been determined.

A high level of transience was observed in females, suggesting that sharks are only using the area for short periods. As the CJS models used are unable to distinguish between mortality and permanent emigration, high levels of transience in the population will result in drastically reduced estimates for survival. Transient individuals, which only visit the site for a short period before permanently leaving, are lumped together with animals that have died, creating an apparent increase in mortality, and corresponding decrease in survival estimates. Therefore, to account for the high level of transience, an age effect constraint was placed on the survival estimates, separating initial observations from subsequent observational periods. This allowed for the survival estimates of individuals which were only observed once to be separated from individuals which were observed

multiple times, to decrease the effect of transience on survival estimates. This resulted in two separate estimates for survival; the first was that for transients and the second for more resident individuals. The survival estimate for transient individuals was much lower than the survival estimate for the individuals observed on multiple occasions. These lower estimates confirm the negative influence of transients on survival estimates.

One would expect the grouping of sampling periods into seasons to decrease estimates of survival, as these estimates refer to survival of longer periods. However, the estimate seasonal survival (96%) was only slightly lower than estimates of monthly survival (97%).Given the high level of transience at this site, this may be due to seasonal grouping of data better accounting for transient individuals. When data are not grouped, an individual which was seen twice in short succession but falling across two sessions (i.e. end of one month and beginning of the next) would not be regarded as a transient. Monthly data would therefore increase the number of theoretically transient individuals being grouped with non-transients, resulting in a decrease in survival estimates for non-transients, which leads to the similar estimates for monthly and seasonal grouped data. Grouping data by season would increase the chance of individuals which were only present for one short period being considered transient, producing a more realistic estimate of true survival.

The difference observed in estimates between transient and non-transient survival, highlights the impact that transient individuals at an aggregation site have on estimates of survival at the site. The seasonal estimate of survival for transients was only 59% across the three months, whereas the estimate for resightings, representing non-transience, was far higher at 96%.

Recapture probabilities were found to differ over time for both monthly and seasonal models, providing evidence of possible seasonality in abundance at the site. Higher recapture probabilities were observed during spring and summer than during autumn and winter (Figure 3.10). Similar patterns were observed in monthly grouped data, with higher values generally estimated during summer and lows being observed during autumn and winter periods. These patterns may be due to

a low level of seasonality observed at the site, with a slightly higher abundance of individuals during summer resulting in increased recapture probability. However, given the short period of this study, it is difficult to make assumptions about seasonal patterns, and long-term observations should be performed to verify these trends. The estimates of recapture probability are also confounded by the number of sampling sessions pooled for each grouping. The number of sampling sessions pooled differed between months, and while the models are able to account for this in the estimates of survival, the estimates of recapture probabilities may have been affected by these discrepancies. This issue may be exaggerated in this study as the number of sampling sessions differed markedly between seasons.

This study, unfortunately, was not able to address certain aspects of the shark's biology which may affect survival. Due to the sampling technique used, data on total length of individuals were not obtained and could therefore not be factored into survival estimates. Total length has previously been shown to influence survival rates of elasmobranches (Bradshaw *et al.* 2007). Additionally, due to the paucity of the data, sex data had to be removed from the analysis, thus the effect of sex on survival could not be examined. Previous studies have shown that males and females display differing habitat use patterns in specific coastal areas (Luciflora *et al.* 2005, Barnett *et al.* 2010c, Williams *et al.* 2011, 2012). If males are more transient at this site, the grouping of male and female data would increase the effect of transient individuals on survival estimates for all sharks at this aggregation site. Therefore, sex could possibly influence survival estimates of the species, by failing to account for the higher transience observed in males.

Future studies should consider the influence of aspects such as size and sex on survival. An expansion of the study area, incorporating additional sites around the Bay, may also help to account for transience in the population, and provide a greater understanding of the survival and movements of sevengill sharks.

3.4.3 – PhotoID

3.4.3.1 – PhotoID as a means of identifying sevengill sharks

Photo identification proved to be an effective means of identifying individual sevengill sharks in their natural habitat. Divers were able to easily approach individuals, seldom eliciting a noticeable behavioural change in response to their presence. This lack of response suggests that the study had little impact on the behaviour of the sharks, and that the results therefore appear fairly unbiased by stress-related factors resulting from sampling efforts.

Apart from additional scarring on the bodies of the sharks, individuals showed little change in appearance over the study period. The addition of white spots was considered to be of little consequence to identifications, as over the time frame of the study new spots remained small and faint in comparison to older spots, allowing for patterns in bold spots to remain observable. Therefore I believe PhotoID is a useful method for studying sevengill sharks in their natural environment over periods of at least three years. Future studies, however, should consider the use of a double-tagging system for verification of the technique (Dudgeon *et al.* 2008). Unfortunately, time and monetary constraints on this project prevented the use of a double-tagging verification.

3.4.3.2 –Comparisons by -eye vs. semi-automated systems

PhotoID by-eye can be a labour intensive task, especially when a large number of individuals are present in the reference database. An alternative to by-eye identification does exist, with the use of semi- or fully-automated identification systems greatly reducing the effort required to match individuals. Such systems have been used on a variety of animals, including a number of species of elasmobranch (Meekan *et al.* 2006, Van Tienhoven *et al.* 2007, Marshal 2008*)*.

Most photoID studies using spot patterns on elasmobranches have made use of a semi-automated identification program called the Interactive Individual Identification System (I^3S), which ranks images according to a match likelihood value. While I^3S has proven a useful tool in a number of studies (Arzoumanian *et al.* 2005, Meekan *et al.* 2006, Speed *et al.* 2007, Van Tienhoven *et al.* 2007),

it is severely limited by the angle at which photographs can be taken (Speed *et al.* 2007). As the program uses a two-dimensional image to assess a three-dimensional object, changes in the angle of incidence of the image can severely decrease the accuracy of the program. I^3S therefore requires images that are taken exactly perpendicular to the shark. While in theory this is possible, in practice taking photographs from the correct angle can prove difficult, particularly on smaller sharks.

In a pilot study (Raw 2009), the accuracy of I^3S for the identification of sevengill sharks was examined. This study showed that when images were taken from the correct angle and multiple reference images were available for each individual, I^3S was fairly accurate, identifying the correct individual in the top ten matches up to 95% of the time. However, if only a single reference image was available, accuracy dropped to 79%. When images taken at an angle of greater than 30 degrees from perpendicular were included in the database, the accuracy dropped to just 50%. Therefore it was considered that only images taken perpendicular to the shark were suitable for semi-automated identification, and even then a fairly high error existed. As the white spots were used for the study, the potential for spot patterns to change over time further detracted from the use of semi-automated identification systems. Black spots were not considered for identification, as they could not be easily distinguished in all individuals.

Therefore, due to the inaccuracy of the software and the loss of data by using only perfect images (up to 50%), I^3S was not used for identification in this study. Instead only by-eye identifications were used, as it allowed for the use of multiple comparisons of different features and for better interpretation of three-dimensional structures.

Chapter 4 – Habitat use and site fidelity of Sevengill Sharks, *Notorynchus cepedianus* at an aggregation site in False Bay, South Africa.

4.1 – Introduction

4.1.1 – Habitat use

Habitat use has been shown to play a significant role in life history traits and extinction risks of chondrichthyans (Garcia *et al.* 2008). However, while it is possible to determine habitat use patterns with considerable accuracy in many terrestrial and some aquatic ecosystems, it is often difficult to quantify habitat use of large marine animals (Heithaus *et al.* 2001). This is due largely to difficulties in observing marine animals in their environment. Habitat studies on sharks have therefore often dealt with broad environmental factors of habitat, such as temperature, salinity and depth, which can be measured remotely. With the use of archival tags, (i.e. acoustic transmitters, or pop-up archival transmitting (PAT) tags), broad-scale habitat use has been investigated for a number of shark species, including, but not limited to, basking *Cetorhinus maximus* (Sims *et al*. 2005), white *Carcharodon carcharias* (Bonfil *et al.* 2005, Bruce *et al.* 2005, 2006), scalloped hammerhead *Sphyra lewini* (Duncan & Holland 2006) and whale sharks *Rhincodon typus* (Wilson *et al.* 2006).

Archival tags focus predominantly on elements of movement within the water column, recording both environmental (i.e. temperature and salinity), and movement (i.e. speed, direction and depth) variables. These tags give little indication of underlying physical habitat in use by a species, particularly when benthic habitats are patchy. While a species' use of the water column is an integral part of its habitat use, one should not ignore the interaction of sharks with the benthos, particularly for species which frequent shallow waters, or forage close to the benthos.

Few studies have looked at fine-scale habitat use of sharks, focusing on the underlying physical habitats. Heithaus *et al.* (2001, 2002) employed the use of a Crittercam, a small camera attached to tiger sharks, *Galeocerdo cuvier*, to investigate habitat use and behaviour. They were able to successfully observe the habitat use of individual tiger sharks fitted with Crittercams, finding

significant preference for shallow seagrass habitats, which they attributed to higher prey availability. Carraro & Gladstone (2006) used underwater transect surveys to investigate the habitat use and preference of ornate wobbegong sharks, *Orectolobus ornatus*. Divers carried out underwater surveys to locate *O. ornatus* and record the habitat in which the individual occurred. This was then compared with relative habitat availability, to determine if the species showed preference for any particular habitat. The study found *O. ornatus* to show preference towards sponge gardens, barren boulders and artificial structures. This preference was attributed to the structural complexity of this habitat which offerd shelter and protection from predators.

Habitat use studies play a central role in the 'ecosystem approach' to conservation which has seen a proliferation of policy commitments in recent years. Knowing where a species will be found is the foundation for many research goals, whether they are to improve conservation management of a species, or simply to understand its ecology or life history (Rice 2005). The habitat structure of a particular environment may limit populations through the availability of resources (Jones & Syms 1998). In order to sustain an animal population, adequate usable resources are required within the habitat being occupied (Manly *et al*. 1993). Despite the perceived importance of habitat in ecological studies, Bell *et al.* (1991) found the subject of habitat structure to be poorly represented in the ecological literature. In a review of over 30 000 papers, across 15 ecological journals, Bell *et al.* (1991) found that only about 0.7% of papers reviewed were devoted to the ecological role of habitat structure. In a more recent review, however, Speed *et al.* (2010) found the influence of physical and biotic factors on habitat selection to be addressed in approximately 75% of the papers reviewed, suggesting increased interest in the subject over recent years.

Little is known about the habitat use of sevengill sharks, with no studies on the species having dealt directly with the physical habitat. A single study to date has investigated fine-scale movements of acoustically tagged sevengill sharks (Barnett *et al.* 2010d). Although not dealing directly with aspects of habitat use, this study did reveal some interesting aspects of the behaviour of sevengill

sharks. The study showed diurnal activity patterns, with increased activity at night, which may be related to foraging behaviour. Previous observations of the foraging behaviour of the species have also suggested them to be predominantly nocturnal foragers (Ebert 1991a), although this has yet to be shown conclusively.

Habitat use has previously been found to be influenced by prey availability and protection in other shark species, including tiger, *Galeocerdo cuvier* (Heithaus *et al.* 2002), and wobbegong sharks, *Orectolobus ornatus* (Carraro & Gladstone 2006). It must be noted, however, that the tiger shark study was conducted on a wider scale than the current study, classifying habitats as shallow or deep, rather than on an ultra-fine scale used for this study. Given the abundant presence of white sharks, *Carcharodon carcharias*, in False Bay, it is also possible that habitat use by sevengill sharks is to some degree influenced by predation risk.

4.1.2 – Site fidelity

Site fidelity refers to the temporal attachment of an individual to a space in its habitat (Carraro & Gladstone 2006) and the return to and reuse of a previously occupied habitat (Switzer 1993). Site fidelity is prevalent in many bird species (Shields 1984, Gavin & Bollinger 1988) and has been observed in mammals (Greenwood 1980, Lewis 1995), reptiles (Stow & Sunnucks 2004, Pitman *et al.* 2008) and fish (Willis *et al.* 2001, Steingrimsson & Grant 2003). Site fidelity is usually attributed to one of three factors: mating, parturition and feeding (Speed *et al.* 2010, Barnett *et al.*2011).

The degree of site fidelity shown by a shark species is influenced by the quality and availability of resources in a particular area (Heithaus 2004), and can range from strict territoriality to nomadism, although territoriality has not been shown in sharks (Heithaus 2004). The quality of a site may, however, not be the sole factor influencing the degree of site fidelity in a species, with factors such as habitat stability, reproductive success, variability of habitat quality within a site and population pressures also playing a role in driving site fidelity (Switzer 1993). Site fidelity can also fall into different temporal scales, including seasonal, long-term, or daily site fidelity (Speed *et al.* 2010).

The study of site fidelity in sharks has traditionally been a challenge to scientists, due to their high levels of mobility in an environment that makes observations difficult (Heuter *et al.* 2004). Site fidelity has been recorded to some degree in a number of sharks, at least for part of their lifecycle, e.g. gray smoothhound *Mustelus californicus*(Espinoza *et al.* 2011), lemon N*egaprion brevirostris* (Di Battista *et al.* 2008) whit- *Carcharodon carcharias* (Anderson *et al*. 2011) and wobbegong sharks *Orectolobus* ornatus (Carraro& Gladstone 2006). Site fidelity has been recorded for sevengill sharks in the South East of Australia (Barnett *et al.* 2011).

Shark nursery grounds are believed to be essential for population persistence (Bonfil 1997). The importance of nursery grounds, together with the relative ease with which juveniles can be handled, has led to research focussing largely on juvenile life stages of sharks (Heupel *et al.* 2007, Speed *et al.* 2010). Philopatry, the tendency for an individual to return to or remain in its birthplace, has been observed in a number of shark species (Heuter *et al.* 2004), including dogfish (*Scyliorhinus canicula* (Sims *et al.* 2001), lemon (Feldheim *et al.* 2002, DiBattista *et al.*2008), and nurse sharks *Ginglystoma cirratum* (Pratt & Carrier 2001). However, little is known about movements and habitat use of sub-adults and adults, once they have left the nursery grounds (Speed *et al.* 2010). Recently, however, the use of passive remote monitoring systems has led to an increase in the number of publications dealing with the movements of larger sharks over greater spatial ranges, although this is still a relatively new research area in shark research.

While the protection of nursery areas is considered useful in the conservation of shark species, the importance of later life stages has been largely overlooked. Evidence is mounting to suggest that life stages outside of the nursery may be more important in terms of population stability and recovery (Kinney & Simpfendorfer 2009). Management practices and the implementation of marine protected areas should therefore not only consider nursery areas, but also link early life stage conservation with management of older individuals residing outside of nurseries (Kinney & Simpfendorfer 2009). An understanding of the movement patterns, connectivity and site fidelity of shark populations is essential for effective management.

Relatively little is known about the movements and site fidelity of sevengill sharks. Barnett *et al.* (2011) monitored the movements of sevengill sharks in Tasmania, Australia, using acoustic monitoring and satellite technology. This study showed both seasonality and site fidelity in sevengill sharks to coastal habitats in Tasmania. Site fidelity was shown not only over a broad area, but rather to specific habitat (Norfolk Bay or Derwent Estuary), over a fine special scale (about 30km). The site fidelity towards these sites was attributed to feeding site fidelity, due to the lack of evidence for mating, pupping or use as a natal site. Intraspecific variation was also noted in seasonality and site fidelity patterns, with females arriving in the area in spring and males only arriving in late summer. Williams *et al*. (2012) collected detailed movement data for 32 acoustically tagged sevengill sharks in and around north-east Pacific Ocean estuarine embayments. The data revealed a distinctly seasonal pattern of estuary use, with individuals moving into Willapa Bay during spring and summer and dispersing to nearshore coastal habitats in autumn. Spatio-temporal of segregation by both size and sex were observed in the Bay, with males and small females using peripheral channels early in the season before joining larger females in the central estuary. Williams *et al.* (2012) noted high degrees of site fidelity to specific sites within an estuary, similar to results observed in Tasmania by Barnett *et al.* (2011). Williams *et al.* (2012) noted that movements of sevengill sharks between estuaries, as far as 1800km from Washington State to California, may support the feasibility of broad-scale coastal movements to known birthing and nursery grounds. To date, no publications to date have dealt with site fidelity of sevengill sharks in South Africa. Again, it must be noted that previous work on sevengill sharks have dealt with movements on a broader scale then the current study, which focuses on the use of a single aggregation site.

4.1.3 – Aims

This study uses *in situ* observations of sevengill sharks to determine fine-scale micro-habitat use by the sharks at an aggregation site within a marine protected area in False Bay, South Africa (Figure 2.1). Resighting histories are also used to investigate the level of short-term site fidelity displayed to the area

4.2 – Methods

4.2.1 – Data collection

4.2.1.1 – Habitat use

Photographs taken for identification of sevengill shark individuals (*Chapter* 3) were used to determine the habitat they were in at the time of encounter. As each individual encountered was photographed from above, the habitat below each individual at the point of encounter could be determined from the photograph (Chapter 4.2.2). Sex data for each encounter were also recorded (Chapter 2.2.2) and linked to each habitat use entry.

4.2.1.2 – Habitat availability

Habitat availability was examined by SCUBA divers following line transects across the study area to ensure true representation of available habitat. Seven transect lines were followed, running parallel to the shoreline (Figure 4.1). Each transect was approximately 150m in length and 10m apart. Due to the size of the area and heterogeneity of the terrain, running physical lines across the site was not feasible; therefore divers used compass bearings to maintain their course. One diver was equipped with a digital camera in an underwater housing, while the second diver was responsible for navigation. Every 10m along each transect line, estimated by the divers by counting the number of kicks taken to move 10m, a photograph was taken of the habitat directly below the diver. This produced a set of control photographs for each transect, which could be examined to calculate habitat availability. As the photographs showed a greater area than shark identification photographs, each habitat availability photograph was subdivided into four equal segments to increase the resolution of available habitat to similar resolution observed in identification photos. Each section was then recorded as a separate available habitat. Segments of habitat that were obstructed from view were disregarded.

Figure 4.1: Study area (0.033km^2, shaded) at the Pyramid Rock site, showing transect lines for habitat availability survey (Google Earth).

4.2.1.3 – Site fidelity

Site fidelity data were extracted from Capture Mark Recapture (CMR) sighting data recording the resighting frequency of each individual for six months following the date of first sighting.

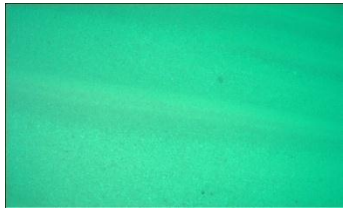
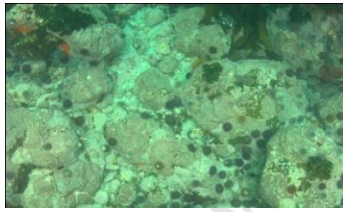
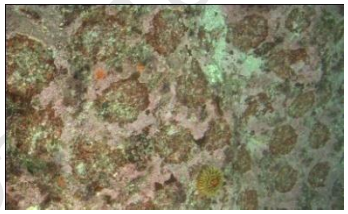
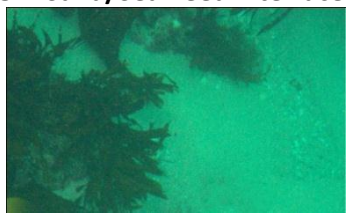
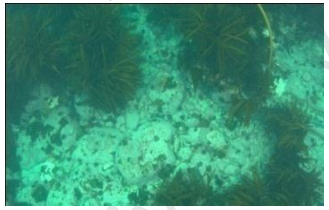
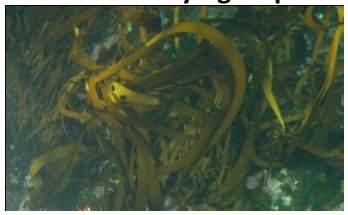
Only individuals first sighted between September 2009 and December 2010 were considered, as these dates allowed for an observational period of at least six continuous months of sampling following each individual sampling session. Data preceding September 2009 were not used in this chapter as a three month gap in sampling prior to September resulted in an incomplete sampling regime for individuals first sighted before this date. An exception was made for individuals first sighted prior to September, but resighted during the chosen observation period. In these cases, the first resighting within the observation period was considered as the effective initial sighting for the purposes of site fidelity analysis. As sampling ended in June 2011, individuals first sighted after December of 2010 did not include a full six month sampling regime and were excluded from analysis.

This process was then repeated for male and female sharks separately. For the sex dependent analysis, only 40 individuals were selected from each sex, and the resighting frequencies again recorded over six months from first observation. Individuals selected for each sex were extracted randomly from the complete dataset (taking into account the same restrictions as above) and not from the subset of individuals used for combined set study.

4.2.2 – Habitat identification

A set of habitat reference images was compiled, each image depicting a particular micro-habitat type, or an interface between two micro-habitat types. Table 2.1 shows the reference set of 15 micro-habitat types used for the study. Interface habitats were further subdivided into one of four categories dependant on the ratios of each micro-habitat type (single habitat, 75:25, 50:50, 25:75).

Table 4.1: Classifications of micro-habitat types encountered at the study site.

1. Sand 	**2. Cobble** 	**3. Rock** 	**4. Sand/Cobble interface** 
5. Sand/Rock interface 	**6. Cobble/Rock interface** 	***7.* Flat rock** 	**8. Sand/Seaweed interface** 
9. Cobble/Seaweed interface 	**10. Rock/Seaweed interface** 	**11. Dense seaweed** 	**12. Sand/Kelp interface** 
13. Cobble/Kelp interface 	**14. Rock/Kelp interface** 	**15. Dense low-lying kelp** 	

Habitat use was then determined from the original, unedited identification photographs. For each encounter the following data were recorded from the photograph:

1. Micro-habitat type
2. Individual identification number
3. Sex of the individual
4. Date
5. Time

Habitat availability was determined from the habitat observed on the control transect survey. The same habitat reference database as for the habitat use was used for habitat availability (Table 2.1).

4.2.3 – Statistical analysis

4.2.3.1 – Habitat preference

Observed habitat use values (number of observations in a particular micro-habitat type) were compared to habitat availability (percentage of a particular micro-habitat in relation to the overall available habitat) to determine selection ratios (Manly *et al.* 1993).

$$\hat{w}_i = \frac{o_i}{\pi_i}$$

Where o_i is the proportion of habitats used that are in category *i*, π_i is the proportional availability of habitat type *i*, and $\hat{w}_i$ is the preference score for habitat type *i*.

Standard error of $\hat{w}_i$ was calculated by

$$SE(\hat{w}_i) = \hat{w}_i \sqrt{\frac{1}{u_i} - \frac{1}{u_+} + \frac{1}{m_i} - \frac{1}{m_+}}$$

Where u_i is the number of sharks in habitat i, u_+ is the total number of observations of sharks, m_i is the frequency occurrence of habitat i, and m_+ is the total occurrence of all habitats.

w_i 95% confidence intervals (CI) calculated by

$$w_i \pm Z_{\alpha/2I} SE_{(Wi)}$$

Where $Z_{(\alpha/2I)}$ is the 100α/(2I) percentage point of the standard normal distribution and I is the number of habitat groups. Bonferroni correction applied by dividing the α significance level(0.05) by the number of habitat groups to allow for multiple comparisons between all habitat categories.

Confidence intervals were used to determine the significance of preference scores. If the upper confidence interval is <1, habitat is significantly avoided. If the lower confidence interval is >1, the habitat is significantly preferred. Lower and upper confidence intervals of <1 and >1 respectively suggest that habitat is used in proportion to its availability. Analyses were run for all individuals combined, as well as for each sex independently.χ^2 tests were used to determine if relative proportions of habitat types differed within interface habitats.

4.2.3.2 – Site fidelity

The frequency distribution of resightings was used to determine the degree of site fidelity. The G-Test was used to calculate the difference in observed frequencies of resightings from the Poisson distribution (Statistica 10. StatSoft Inc.). A Poisson distribution was used as no significant difference between observed frequencies and the Poisson distribution would indicate that resightings are randomly distributed and that the majority of individuals were unlikely to be in the area for the duration of the observation period (Carraro & Gladstone 2006).

Expected Poisson distribution was calculated using the following equation

$$f(k: \lambda) = \frac{\lambda^k e^{-\lambda}}{k!}$$

Where *k* is the number of occurrences of an event, and λ is the expected number of occurrences in a given timeframe (mean of observed values).

4.3 – Results

4.3.1 – Habitat use

A total of 1170 habitat use observations were made between February 2009 and July 2011. Of these, 672 were observations of females, while only 90 were observations of males. The remaining 408 observations were for individuals of unknown sex. The number of occurrences of each habitat type is shown in Figure 4.2.

A total of 134 habitat availability photographs were taken, resulting in 536 segments. Two segments were obscured from view and were excluded from the analysis.

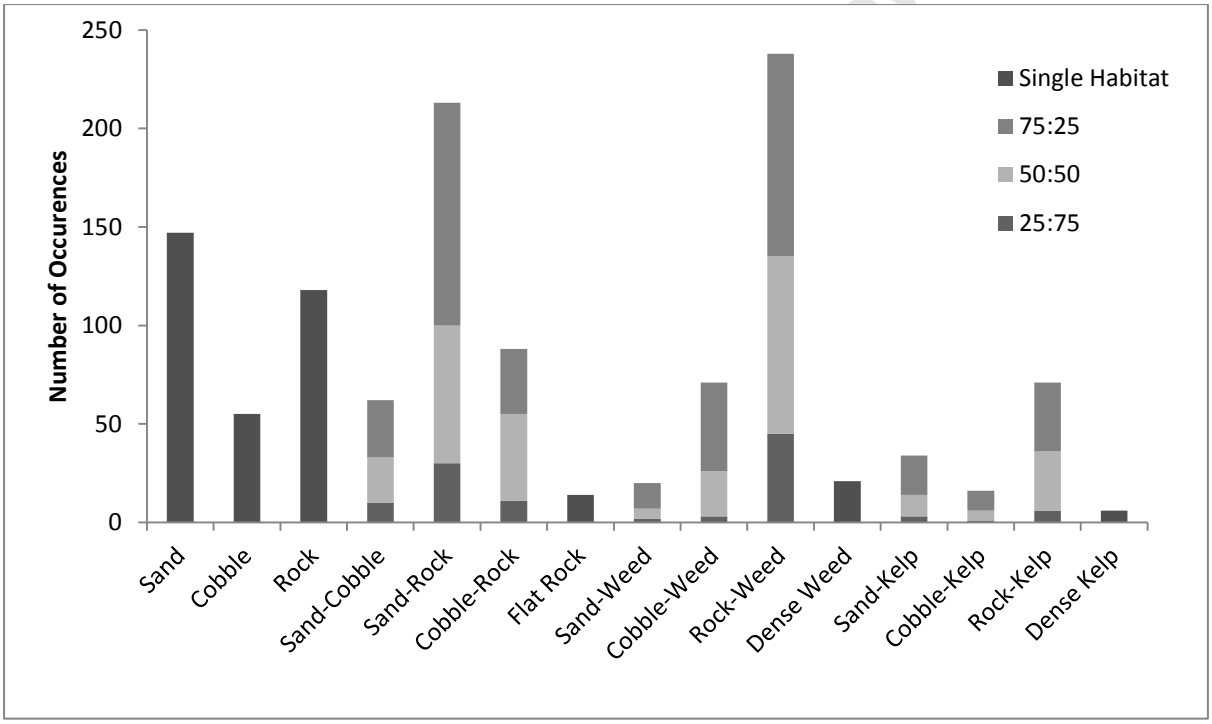


Figure 4.2: Number of occurrences of individual sharks in each habitat type, with each interface habitat subdivided by relative percentages of each habitat. Ratios of habitat type relate to the order named on x-axis.

4.3.1.2 – Overall habitat use

Preference was shown for the interface between sandy and rocky areas ($\hat{w}_i$=1.8, SE = 0.258, lower CI = 1.044, α = 0.05). Within the sand-rock interface habitats, significantly more individuals were observed in the 75:25 subdivision of predominantly sand (χ^2 = 48.5, *df* = 2, p < 0.005) than for the 25:75 and 50:50 divisions. This suggests the sharks remain more on the sand side of the interface than the rock side. The availability of sand-rock habitat also showed significant differences between proportions of sand and rock (χ^2 =7, *df* = 2, p < 0.05), with the 25:75 subdivision being significantly lower than expected with equal distribution. Some level of preference was also shown for sand-cobblestone ($\hat{w}_i$ =4.488, SE = 1.909, lower CI = 0.0, α = 0.05) and cobblestone-rock ($\hat{w}_i$ =3.347, SE = 1.015, lower CI = 0.368, α = 0.05) interfaces, although due to the relatively low sample sizes of these habitats, they did not show as significant. However, the proportionate use of these habitats was over double their availability (Figure 4.3).

Avoidance was observed for the interfaces between both sand-kelp ($\hat{w}_i$ = 0.293, SE = 0.062, upper CI = 0.476, α = 0.05) and rock-kelp ($\hat{w}_i$ = 0.395, SE = 0.061, upper CI = 0.573, α = 0.05). All other habitats were used proportionally to their availability. Values of habitat use selection indices are summarised in Table 4.2.

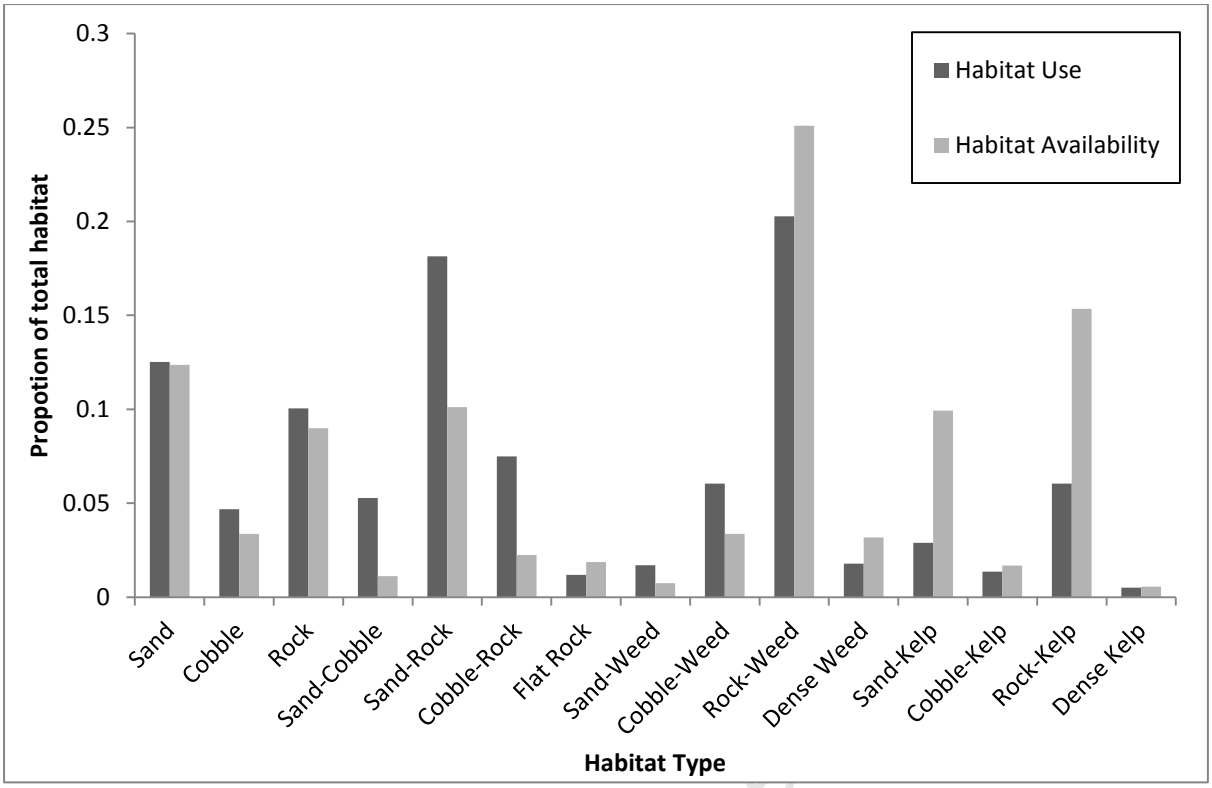


Figure 4.3: Comparisons between observed habitat use and habitat availability for each habitat class.

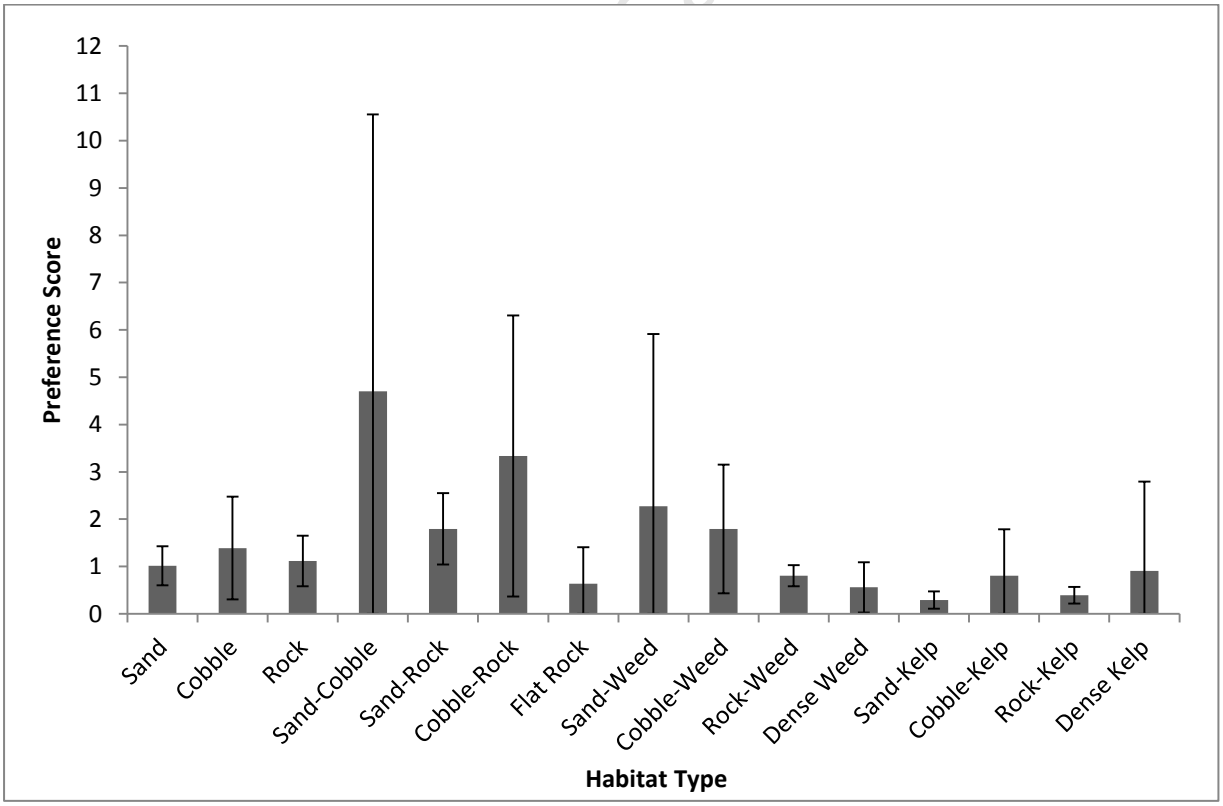


Figure 4.4: Habitat preferences of all sevengill sharks. Preference scores and their 95% confidence intervals are shown for each habitat. Habitat preference scores with lower confidence intervals >1 show significant preference; upper confidence intervals <1 indicates significant avoidance. All other values indicate no preference.

4.3.1.3 – Habitat use between sexes

No habitat preference was shown by female sevengill sharks, however, avoidance was observed for the interfaces between both sand-kelp ($\hat{w}_i$ = 0.360, SE = 0.086, upper CI = 0.612, α = 0.05) and rock-kelp ($\hat{w}_i$ = 0.455, SE = 0.079, upper CI = 0.687, α = 0.05). Values of habitat use selection indices for female sevengill sharks are summarised in Table 4.3.

No habitat preference was shown by male sevengill sharks, however, avoidance was observed for the interfaces between sand and kelp ($\hat{w}_i$ = 0.224, SE = 0.159, upper CI = 0.691, α = 0.05). Values of habitat use selection indices for male sevengill sharks are summarised in Table 4.4.

Table 4.2: Habitat use, availability and selection indices for all sevengill sharks observed in a kelp forest environment, where U_i is the number of sharks in habitat *i*, O_i is the proportion of sharks in habitat *i*, m_i is the frequency occurrence of habitat *i*, π_i is the relative proportion of habitat *i,* $\hat{w}_i$ is the selection index for habitat *i and* B_i is the relative proportions of $\hat{w}_i$. Significant values are shown in bold.

								Confidence limits	
Habitat Class	U_i	O_i	m_i	π_i	$\hat{w}_i$	B_i	$SE(\hat{w}_i)$	*Lower*	*Upper*
Sand	147	0.126	66	0.124	1.017	0.047	0.141	0.603	1.430
Cobblestone	55	0.047	18	0.034	1.395	0.064	0.372	0.304	2.485
Rock	118	0.101	48	0.090	1.122	0.052	0.183	0.585	1.659
Sand-Cobblestone	59	0.050	6	0.011	4.488	0.207	1.909	0.000*	10.09
Sand-Rock	**213**	**0.182**	**54**	**0.101**	**1.800**	**0.083**	**0.258**	**1.044**	**2.557**
Cobblestone-Rock	88	0.075	12	0.022	3.347	0.154	1.015	0.368	6.326
Flat Rock	14	0.012	10	0.019	0.639	0.029	0.262	0.000*	1.410
Sand-Weed	20	0.017	4	0.007	2.282	0.105	1.244	0.000*	5.934
Cobblestone-Weed	71	0.061	18	0.034	1.800	0.083	0.466	0.433	3.167
Rock-Weed	237	0.203	134	0.251	0.807	0.037	0.076	0.583	1.031
Dense Weed	21	0.018	17	0.032	0.564	0.026	0.182	0.0308	1.097
Sand-Kelp	**34**	**0.029**	**53**	**0.099**	**0.293**	**0.014**	**0.062**	**0.109**	**0.476**
Cobblestone-Kelp	16	0.014	9	0.017	0.811	0.037	0.335	0.000*	1.796
Rock-Kelp	**71**	**0.061**	**82**	**0.154**	**0.395**	**0.018**	**0.061**	**0.217**	**0.573**
Dense Kelp	6	0.005	3	0.006	0.912	0.042	0.644	0.000*	2.802
Totals	1170	1	534	1	21.673	1			

*Negative lower confidence intervals have been replaced by 0.000 since negative values for the selection indices are impossible.

Table 4.3: Habitat use, availability and selection indices for female sevengill sharks observed in a kelp forest environment, where U_i is the number of female sharks in habitat *i*, O_i is the proportion of sharks in habitat *i*, m_i is the frequency occurrence of habitat *i*, π_i is the relative proportion of habitat *i,* $\hat{w}_i$ is the selection index for habitat *i and* B_i is the relative proportions of $\hat{w}_i$. Significant values are shown in bold.

								Confidence limits	
Class	U_i	O_i	m_i	π_i	$\hat{w}_i$	*Bi*	*SE(* $\hat{w}_i$*)*	*Lower*	*Upper*
Sand	65	0.097	66	0.124	0.783	0.039	0.129	0.404	1.161
Cobblestone	35	0.052	18	0.034	1.545	0.077	0.439	0.256	2.834
Rock	72	0.107	48	0.090	1.192	0.059	0.211	0.572	1.812
Sand-Cobblestone	32	0.048	6	0.011	4.238	0.211	1.869	0.000*	9.725
Sand-Rock	104	0.155	54	0.101	1.530	0.076	0.241	0.823	2.237
Cobblestone-Rock	35	0.052	12	0.022	2.318	0.116	0.764	0.076	4.559
Flat Rock	6	0.009	10	0.019	0.477	0.024	0.245	0.000*	1.195
Sand-Weed	9	0.013	4	0.007	1.788	0.089	1.069	0.000*	4.927
Cobblestone-Weed	47	0.070	18	0.034	2.075	0.103	0.562	0.424	3.726
Rock-Weed	171	0.254	134	0.251	1.014	0.051	0.101	0.717	1.311
Dense Weed	11	0.016	17	0.032	0.514	0.026	0.197	0.000*	1.092
Sand-Kelp	**24**	**0.036**	**53**	**0.099**	**0.360**	**0.018**	**0.086**	**0.107**	**0.612**
Cobblestone-Kelp	11	0.016	9	0.017	0.971	0.048	0.433	0.000*	2.242
Rock-Kelp	**47**	**0.070**	**82**	**0.154**	**0.455**	**0.023**	**0.079**	**0.223**	**0.687**
Dense Kelp	3	0.004	3	0.006	0.795	0.040	0.647	0.000*	2.694
Totals	672	1	534	1	20.055	1			

*Negative lower confidence intervals have been replaced by 0.000 since negative values for the selection indices are impossible.

Table 4.4: Habitat use, availability and selection indices for male sevengill sharks observed in a kelp forest environment, where U_i is the number of male sharks in habitat *i*, O_i is the proportion of sharks in habitat *i*, m_i is the frequency occurrence of habitat *i*, π_i is the relative proportion of habitat *i,* $\hat{w}_i$ is the selection index for habitat *i and* B_i is the relative proportions of $\hat{w}_i$. Significant values are shown in bold.

								Confidence limits	
Class	U_i	O_i	m_i	π_i	$\hat{w}_i$	*Bi*	*SE(* $\hat{w}_i$*)*	*Lower*	*Upper*
Sand	8	0.089	66	0.124	0.719	0.035	0.256	0.000*	1.472
Cobblestone	3	0.033	18	0.034	0.989	0.047	0.606	0.000*	2.768
Rock	6	0.067	48	0.090	0.742	0.036	0.310	0.000*	1.651
Sand-Cobblestone	4	0.044	6	0.011	3.956	0.190	2.513	0.000*	11.332
Sand-Rock	16	0.178	54	0.101	1.758	0.084	0.459	0.412	3.104
Cobblestone-Rock	8	0.089	12	0.022	3.956	0.190	1.748	0.000*	9.087
Flat Rock	0	0.000	10	0.019	0.000	0.000	0.000**	0.000**	0.000**
Sand-Weed	2	0.022	4	0.007	2.967	0.142	2.547	0.000*	10.442
Cobblestone-Weed	2	0.022	18	0.034	0.659	0.032	0.486	0.000*	2.085
Rock-Weed	26	0.289	134	0.251	1.151	0.055	0.209	0.538	1.765
Dense Weed	1	0.011	17	0.032	0.349	0.017	0.357	0.000*	1.397
Sand-Kelp	**2**	**0.022**	**53**	**0.099**	**0.224**	**0.011**	**0.159**	**0.000***	**0.691**
Cobblestone-Kelp	1	0.011	9	0.017	0.659	0.032	0.691	0.000*	2.687
Rock-Kelp	10	0.111	82	0.154	0.724	0.035	0.228	0.055	1.393
Dense Kelp	1	0.011	3	0.006	1.978	0.095	2.273	0.000*	8.648
Totals	90	1	534	1.000	20.830	1.000			

*Negative lower confidence intervals have been replaced by 0.000 since negative values for the selection indices are impossible.

**Lack of observations of males in flat rock habitat resulted in null values for the calculation of standard error.

4.3.2 – Site fidelity

A total of 353 individual sevengill sharks were identified for analysis of site fidelity, comprising 551 observations, with 122 individuals resighted at least once. The average proportion of resightings was 0.56. Of the 353 individuals examined, 231 were not resighted again within six months of first observation. The greatest observed number of resightings for a single individual within the six month period was five. The frequency distribution of resightings (Figure 4.5) differed significantly from an expected Poisson distribution (G = 50.989, *df* = 5, P < 0.001) and was skewed towards the left and had a single mode. The frequency of no resightings was above expected, as were the frequencies for 3-5 resightings. Resighting frequencies for 1-2 resightings were below expected values.

From the 40 females used for the sex dependent analysis, a total of 105 observations were made, with 30 individuals resighted at least once within six months of initial observation. From the males, only 45 observations were made, with only four individuals resighted, only one of which was resighted more than once. Approximately 90% of males were not resighted within six months of first observation, and only 15% were ever resighted again over the remainder of the study.

Neither the distribution of female (G= 5.4, *df* = 7, P > 0.05) nor male (G= 1.7, *df* = 7, P > 0.05) sevengill sharks differed significantly from a random Poisson distribution. The distribution of resightings was less skewed for females (Figure 4.6) than for both sexes combined (Figure 4.5) or males only (Figure 4.7) data.

Females showed similar discrepancies to the Poisson distribution as observed in the combined dataset, with higher values for lower resighting rates, lower values for midrange resighting values and higher values for higher resighting rates.

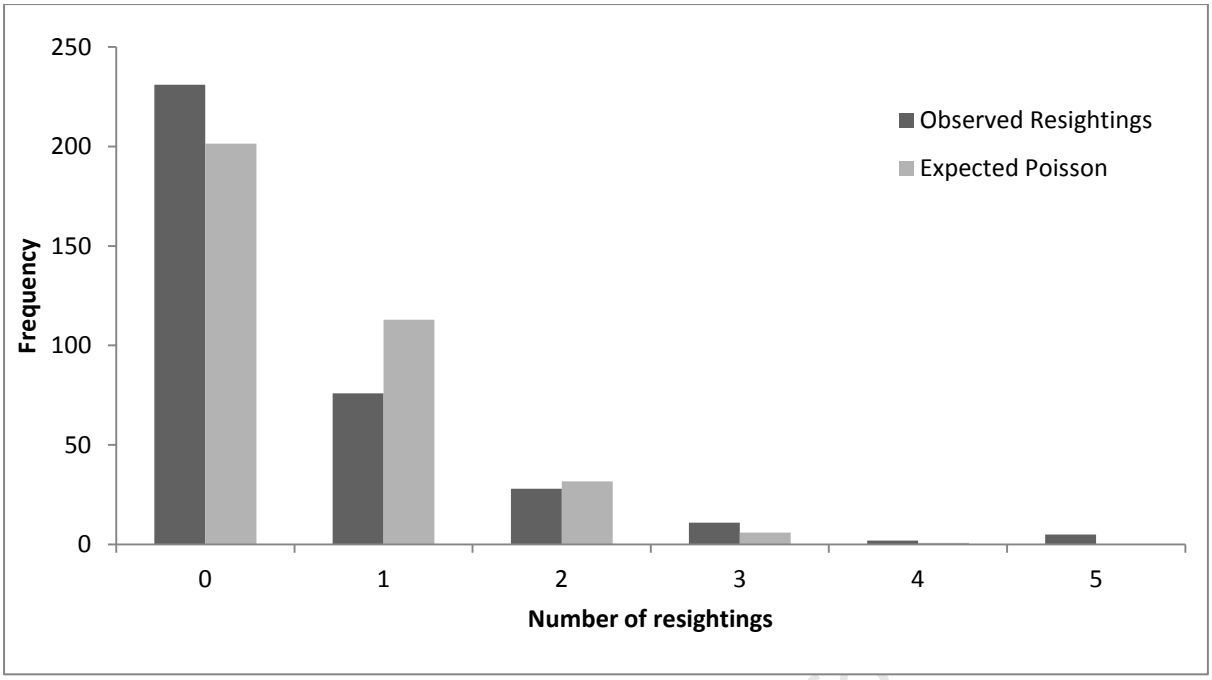


Figure 4.5: Frequency distribution of all sevengill shark resightings over six months from first observation and the Poisson distribution assuming resightings are randomly distributed. N=353.

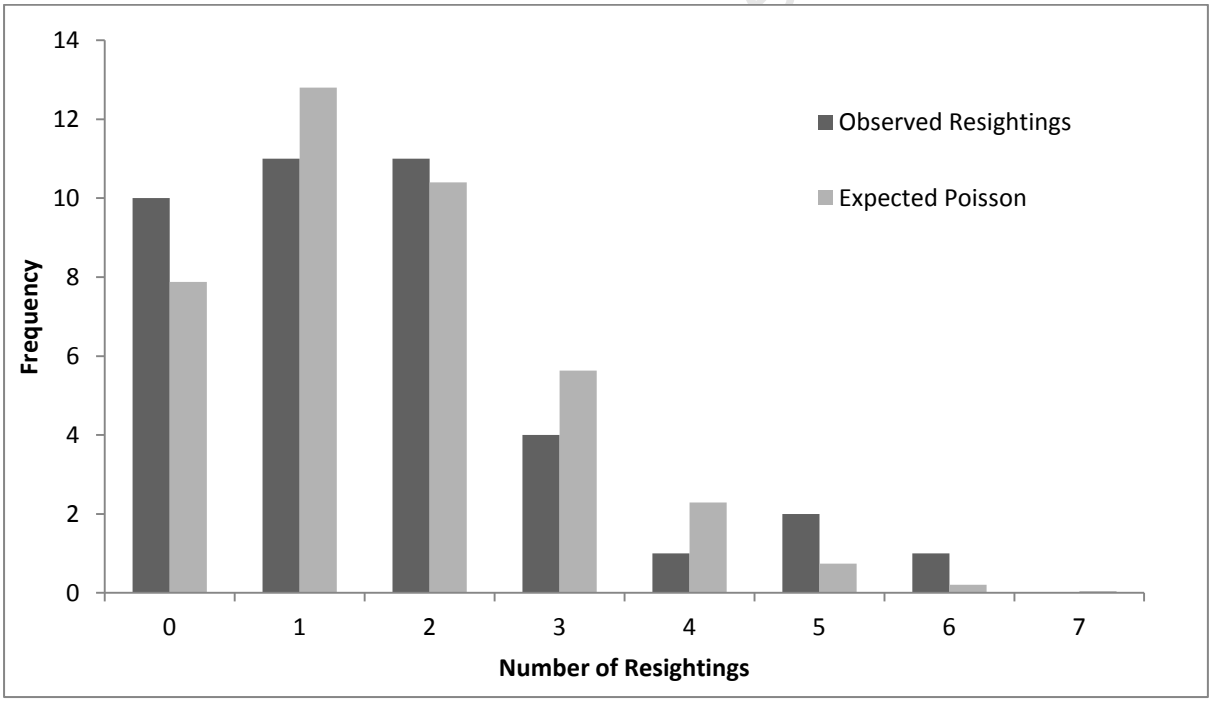


Figure 4.6: Frequency distribution of female sevengill shark resightings over six months from first observation and the Poisson distribution assuming resightings are randomly distributed. N=105.

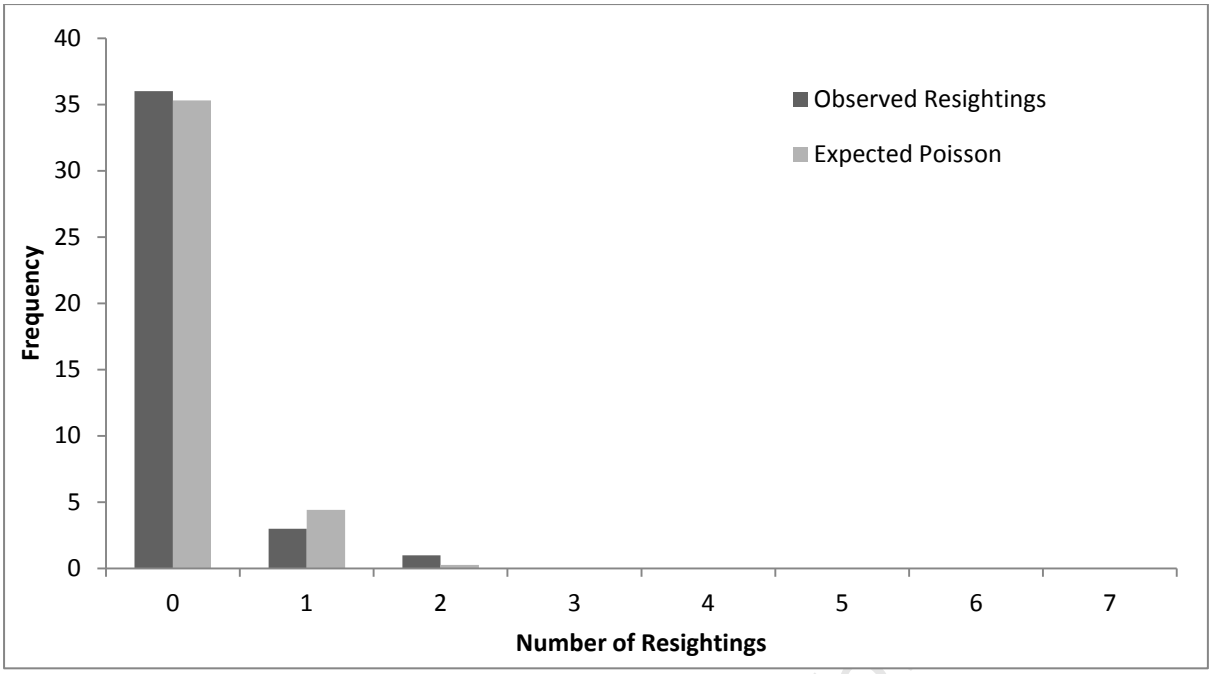


Figure 4.7: Frequency distribution of male sevengill shark resightings over six months from first observation and the Poisson distribution assuming resightings are randomly distributed. N=45.

4.4 – Discussion

4.4.1 – Habitat use

Habitat use data at the aggregation site showed the highest number of individuals found along the interface between rock and low lying seaweeds, followed closely by individuals along the interface between rock and sand. However, these values alone do not take into account the availability of these micro-habitats in relation to other habitat types in the area. Therefore, the high number of individuals observed along the rock-weed interface may be a result of that particular micro-habitat occupying much of the available habitat. The rock-weed micro-habitat, is the most abundant micro-habitat at the site (over 25%), suggesting that the high use of the micro-habitat may simply reflect relative availability.

However, habitat preference analysis showed that the rock-weed micro-habitat was in fact used less than one would predict based purely on availability, suggesting that although it is the most abundant micro-habitat, it is not preferred by sevengill sharks in False Bay. In contrast, the usage of

the sand-rock interface, which only occupies approximately 10% of the available habitat, under half that the rock-weed interface, was almost as high as for the rock-weed interface, suggesting preference for the sand-rock micro-habitat over the rock-weed micro-habitat. Preference was also shown for sand-cobblestone and cobblestone-rock interfaces, both of which had fairly low availability, but relatively high levels of usage. These three micro-habitats are all dominated by low-lying substratum, namely sand and cobblestone, and where rocky substratum was involved, most of the individuals were observed on the sand or cobblestone side of the divide.

Over the course of this study, no observations of foraging were made at the site, instead the behaviour of the sharks was fairly docile and inactive(pers. obs.), probably due to the study being conducted during daylight hours, while sevengill sharks are thought to be predominantly nocturnal foragers (Ebert 1991a, Barnett *et al.* 2010d). However, the possibility that sevengill sharks may opportunistically feed during daylight hours at this aggregation site cannot be completely disregarded. A recent study has shown daytime movement patterns which could be indicative of daytime foraging behaviour in a population of sevengill sharks in Tasmania (Barnett *et al.* 2010d). The possibility of daylight foraging in the species could link habitat preference of sevengill sharks at this site to prey availability. Ebert (1991b) found chondrichthyans to be the most important prey group in the diet of sevengill sharks in the Western Cape, including the pyjama catshark, *Poroderma africanum*, and the leopard catshark, *P. pantherinum*, both of which were commonly sighted in the study area. However, the fact that numerous potential prey items were observed in close vicinity to sevengill sharks, yet no predation attempts were observed, suggests that this site is not being used for foraging during the day.

If the sharks are not using the site for foraging during the day, the driving force behind this aggregation may be shelter from predators. False Bay is home to a large resident population of white sharks, placing a large potential threat on sevengill sharks. This threat is evident by large scars and fresh wounds (clean cut, circlar bitemarks) observed on some individuals, which appear to be a

possible result of an encounter with a white shark (pers. obs.). Previous observations of the habitat choice of sevengill sharks in Tasmania, showed sevengill sharks, Among other areas, to frequently use open sandy areas (Barnett *et al.* 2010d). Given this, one might expect to find aggregations of sevengill sharks along the northern shores of False Bay, where the habitat is open and sandy. However, sevengill sharks are seldom observed in these areas (Lamberth 2006), but rather observed in abundance at the study site, which is relatively closed, rocky and dense with kelp. The pyramid rock site may therefore provide shelter from these predators, which frequent open, inshore, sandy areas during summer (Kock *et al.* 2012).

The complexity of the habitat at Pyramid Rock, consisting of large boulders, some of which extend above the surface, sandy gullies, rock and cobble stone seafloor, as well as areas of dense kelp, may provide shelter from predators, with greater chance of escape if a predator is encountered then more open sites. The sharks may therefore be using the complex structure of the habitat at this site to provide themselves with the best overall protection from predators, attracting individuals to aggregate at this site during the day. Heithaus *et al.* (2009) noted that tiger shark prey shifted their habitat use to edge-habitats when shark abundance increased, despite shark abundance being higher in these areas. They suggest anti-predator behaviour to therefore be based on overall risk assessment, rather than making habitat choice based purely on a single factor, such as predator abundance. In this case, edge-habitats may offer greater escape success to prey items attempting to avoid a predator than other seemingly more productive areas with lower shark densities.

If the site is being used for predator avoidance during the day, it seems counter-intuitive that the sharks would avoid micro-habitats along the edge of low-lying kelp, as the kelp may provide additional shelter from predators. However, the avoidance of areas consisting of low-lying kelp may be linked to a physical barrier created by the kelp. The low-lying kelp examined in this study its fairly dense and generally within 1 m from the sea floor and may, therefore, act more as a hindrance to an escape, restricting movement without providing sufficient cover in return. The structural complexity

of all the micro-habitats, coupled with the protection from the upper kelp canopy, may offer sufficient cover to allow individuals to utilize the more open micro-habitats, such as sand, cobblestone and rock beds, to allow free movement through the site, while still benefiting from the shelter offered by the kelp and larger rocks.

Few differences were observed between the habitat use of males and females. Although neither male nor female sevengill sharks exhibited any significant levels of habitat preference when separated (Tables 4.3 & 4.4), both sexes were still observed use the sand-cobblestone, sand-rock, and cobblestone-rock habitats in greater proportion than their availabilities, suggesting that both sexes are making similar use of the available habitat while at the site.

The only major difference observed between the habitat uses of each sex was in the use of the rock-kelp interface. While females showed avoidance of this micro-habitat, males used this micro-habitat in proportion to its availability. Anecdotal evidence suggests males at the site to be generally smaller than females (pers. obs.). If this is the case, the increased use of rock-kelp micro-habitat by males may be linked to their smaller size, as smaller individuals would be better suited to navigating through kelp. An alternative hypothesis could be that intraspecific competition for space forces them into unfavourable micro-habitats. However, without quantitative size data one is unable to make conclusions on the matter.

If the driving force behind this aggregation site is protection from predators, one would expect high residency rates for individuals using this site. However, as the residency rates are low, it is less likely that protection from predation alone attracts individuals to this site. Another possibility to consider is the use of the site for social interactions. Pyramid Rock may be a mating site for the species, attracting individuals to aggregate to facilitate copulation. Pratt & Carrier (2001) found that adult nurse sharks, *Ginglymostoma cirratum*, use a shallow lagoon, away from the main reefs, for reproductive purposes, seasonally migrating to a small mating site to reproduce. Despite the presence of potential prey, no evidence of adult feeding has been observed in the lagoon. They

speculate that adult females use the site as a mating refuge for reproductively active females, as excessive attention from males and competition on the reef could jeopardize their fitness or reproductive success. Although copulation by sevengill sharks has not been observed at the Pyramid Rock site, fresh bite marks (differing from the potential white shark bites mentioned previously) on the flanks of many of the large females observed at the site indicate recent mating activity. It may also be possible that females are using this site as a refuge from excessive male attention, allowing them time to rest and recover from mating behaviours, while still offering protection from predators. Alternatively, the site my offer protection from predators such as white sharks while breeding.

4.4.2 – Habitat use conclusions

The use of the Pyramid Rock site appears to be largely as a resting area during the day. While the most commonly used habitat was along the rock-weed interface, this micro-habitat was in fact used less than its proportion of the overall available habitat. Preference was rather shown for more open micro-habitats, such as sand, cobblestone and rock, which allow individuals to move unrestricted through the area while resting during the day. The complexity of the habitat at the site is likely to offer protection from predation, allowing individuals to move freely through these open habitats, while still benefiting from the shelter provided by surrounding habitats.

Due to the methods of recording habitat use using photographs taken downwards, only low-lying kelp (the undergrowth of the kelp forest canopy) was considered in the analysis. While using only low-lying kelp can account for much of the effect of kelp on the habitat use of sevengill sharks (physical barriers, shelter, resource availability), the upper canopy also plays a role in the overall workings of the ecosystem. The sea bamboo, *Ecklonia maxima,* which form the upper canopy of the kelp forest, only reaches down to the sea floor with a relatively thin stipe, however, the upper canopy can be fairly dense, affecting light penetration and acting as a barrier or deterrent to potential predators. As only low-lying kelp was recorded, areas recorded as being free of kelp may

still have been influenced by an upper kelp canopy. Future studies should consider a method of recording both understory kelp and the upper canopy, to determine if canopy cover has an effect on habitat preference.

A further drawback to the study is the small size of the study area. When a habitat occupies only a small space in an area, it becomes difficult to confidently state whether preference was shown for that habitat, or the apparent preference may be an artefact of other factors, possibly that of adjacent habitats. For instance, if the small region of sand-cobblestone habitat was placed predominantly next to sand-rock habitats, the apparent preference for sand-cobblestone habitat may be an artefact of sharks using the sand-rock habitat simply passing through an area where the rock becomes cobblestone. The preference may therefore not necessarily be for cobblestone, but rather just by chance due to its location in regards to rocky areas. In order to account for this, one would need to sample a larger area, increasing the number of occurrences of the habitat to determine if the apparent preference is real, or an artefact of a small sample size.

This study only looked at a single element of habitat, that of the underlying substratum. Marine habitats, however, are three-dimensional environments, influenced by a broad spectrum of environmental factors, including depth, temperature, salinity, visibility and surge. In order to fully understand the causes underlying habitat selection in a marine species, it is necessary to investigate multiple aspects of the environment. Unfortunately, constraints of time and resources for this study limited the ability to investigate additional aspects of habitat use. Future work should include the integration of acoustic telemetry systems, together with observational data to gain a more complete understanding of habitat use by sevengill sharks.

As sevengill sharks are thought to be predominantly a nocturnally active species, future studies might look to conduct night-time surveys of the population, to determine how the sharks are using the area at night. Such observations could answer questions regards the driving forces behind the use of this site, such as, is the site used as a feeding or mating ground, or do the sharks move out of

the area at night to feed, returning to rest during the day? Night dives, however, should be approached with caution, as sevengill sharks are potentially dangerous to humans and it is unknown how they might react to human contact during their nocturnal foraging activities. Nocturnal observations mayalso be done using tracking techniques, including both passive and active monitoring.

A potential bias of using civilian divers for data collection needs to be considered in the evaluation of habitat preference results. As the dives were largely aimed at finding sharks to please clients, the results may be influenced by diver preference of habitat, with samples not being taken at random. As some divers prefer to avoid dense kelp, part of the avoidance for kelp interface habitats may be linked to diver bias. The tendency of eco-tour operators to focus on areas in which sharks are frequently seen may be testament in itself for shark habitat preference, however the effect of diver bias must be considered when drawing conclusions from these results. The effect of bias from the use of civilian science is discussed further in chapter five.

4.4.3 – Site fidelity

Site fidelity plays an important role in conservation planning, in particular the designation of marine protected areas (MPAs), as the frequency with which a species uses a particular area can influence the effectiveness of a protective area. As the study site is situated in an MPA, the site fidelity of sevengill sharks to the site can give insight on the influence the MPA may have on the species.

Short term site fidelity for the Pyramid Rock site was fairly low, with a large proportion of the population only sighted once over the six months. The low average number of resightings suggests a high level of transience in the population, with a high turnover of individuals and many of the individuals observed at the site only staying for short periods of time. This finding agrees with findings from Chapter 3, where the distinctly linear discovery rate observed in the discovery curve for the study (Figure 3.6) suggests the site is visited by individuals from the greater population, with

a high turnover of individuals. Females were resighted more often within the six month period than males, suggesting that females have greater residency times, while males only visit the site for brief periods before moving on, showing males to be far more transient then females.

As site fidelity is usually driven by one of three factors: mating, parturition and feeding (Speed *et al.* 2010), the difference in site fidelity between male and female sevengill sharks may be linked to the reasons for the use of this area. Although size data were not recorded in this study, observations using visual estimates of total length suggested that all individuals were at least medium to large in size (> 1m TL), with no new born (< 50cm TL) individuals observed at the site. The lack of new-borns at the site and the lack of evidence of foraging, in particular during daylight hours, suggest that it is unlikely that site fidelity is driven by parturition or feeding.

The use of this site this therefore most likely linked in some degree to mating. Fresh scars observed on the flanks of many of the sharks, in particular large females, suggest recent mating activity. Again, no observations of mating behaviour have been made, but the presence of mating scars confirms recent mating, although it is impossible to say whether the mating occurred at the site or elsewhere, with individuals moving to the site after the act. Mating scars have previously been shown to be a valid means of determining mating activity in elasmobranches (Kajiura *et al.* 2000). Seemingly gravid females were also observed during the study, with extended abdomens and healing mating scars on their flanks. Although it is possible that the extension of the abdomen was due to a recent large meal, the lack of abdomen extension of this kind in males suggests that it is not related to food. It may be possible that this site is used by gravid females after mating, later moving to a nursery/pupping area to pup. This would support the notion that females are using the area as a refuge from both the attention from males and from predation, spending longer periods within the site and returning more frequently than males. This idea is supported by the extreme sex bias towards females observed at the site. The higher levels of transience observed in males at the site

may therefore be linked to males coming into the area to explore mating opportunities while the females are aggregating.

4.4.4 – Site fidelity conclusions

Site fidelity was fairly low, with high levels of transience in both males and females. The factors driving the difference in site fidelity between males and females remain unclear; however, the higher level of site fidelity in females may be linked to females taking refuge at the site, therefore spending longer periods and returning more frequently.

Future studies should incorporate size data into the analysis, to determine whether site fidelity is influenced by size, with individuals of different size classes showing different levels of site fidelity. Observations of night time behaviours could also help clarify the underlying cause for individuals aggregating at this site. Passive monitoring, with the use of acoustic or satellite tags should also be incorporated into future studies. Passive monitoring will provide greater resolution of movements, allowing for the movements of individuals to be tracked over greater distances and time frames than would be possible with in situ observations. This may help identify other areas commonly used by sevengill sharks, to answer questions on the use of the Bay.

Chapter 5 – Conclusions

5.1 – Population demographics

The effective conservation of a species is best managed from a strong ecological foundation (Arzoumanian *et al.* 2005). This requires knowledge of not only the life-history of a species, but also its demographics, movement patterns and habitat use.

Until recently, the focus of research on sevengill sharks has been on life-history traits, in particular sexual maturity, growth and feeding. While these are all important factors to consider in the conservation of the species, without information on the demography of populations it is difficult to judge the true resilience of the population. In addition, knowledge on the extent of movements and habitat use of the population are vital in specifying important areas for the protection of important life stages of the species.

This study has provided some of the first estimations of survival of sevengill sharks, as well as insight into fine-scale micro-habitat use, seasonality, site fidelity, and sex structure of a population that aggregates at a site within a marine protected area.

A total of 587 individual sharks were observed and identified over the course of the study. While this may seem like a high number of individuals to be observed at a single location, the consistent rate of discovery suggests that this is just a fraction of the super-population. It appears that individuals from the super-population move into the area for relatively short periods before moving on, resulting in a high level of transience at the site. The high level of transience was stressed throughout the analyses of the mark recapture data, including discovery rates, survival and site fidelity. Some discrepancies where observed in the levels of transience, in particular relating to sex. Tests for transience in the analyses of survival suggested high levels of transience for females, but not for males. Site fidelity analysis, on the other hand, suggested males exhibit higher levels of transience, with fewer males ever resighted then females. This, however, may be due to the low

sample size of males. Only 66 males were observed, with a total of only 91 observations. With such a small sample size and so few resightings, it is difficult for the software to distinguish transience with any significance.

Due to the high level of transience, short-term site fidelity was fairly low, with few individuals remaining in the area for prolonged periods. Females, however, did show a higher frequency of resightings than males, supporting the notion of males being more transient. Females also were resighted more frequently following the six months analysed for site fidelity, suggesting that females use the site more frequently. Although highly transient, some individuals do show signs of fidelity over longer periods, suggesting a possibly return to the site linked to the reproductive cycle. Therefore, considering the low number of resightings for males it appears that males are highly transient.

The population also showed to have highly skewed sex ratios, with females outnumbering males at the site 4.1 to 1. This is likely due to females using the inshore areas more than males, with males coming inshore less frequently and for shorter periods.

Survival estimates were limited by the high level of transience at the site, creating an open population. An open population results in estimates of survival that are greatly affected by emigration, and not true estimates of survival. Thus models had to be constrained to account for individuals which were only present in the area for a short period and never seen again. This resulted in two separate estimations of survival, one for transient individuals and a second for non-transients. Seasonally grouped data were found to better account for transient individuals, producing more realistic estimates of survival. Survival for non-transients was far higher than for transients, due to the high level of permanent emigration in transient sharks.

Although modes separated highly transient individuals from non-transient individuals, there is little evidence of resident individuals at this site. It is more likely that individuals categorized as non-

transient in fact displayed some level of transience, but returned to the site more frequently. Longer observations and the inclusion of other biological data, such as size and age structures, may help reveal if different aged, sized or sexed individuals show different levels of transience, and furthermore, different survival rates.

Discussion with locally-based divers revealed that a number of areas around the Western Cape are known for relatively common sightings of sevengill sharks, however, there are no reported sites at which sevengill sharks can be observed by divers in their natural habitat so regularly and in such abundance as the Pyramid Rock site. Over the past three years of this study, an average of 16 individuals have been observed per dive, with not a single dive having been conducted at the site with no shark sightings. In addition, these observations were made without the aid of chum or bait, allowing researchers to observe the sharks in their natural environment, without disturbing their natural behaviour. This makes the site the perfect location for the study of the behaviour of the species and should continue to be monitored to obtain long term data on behaviour.

The reasons driving the use of this site by so many individuals still remain unclear. With an average of over 16 sharks observed per session, the observation rate at this site is higher than any reported for any other aggregation of sevengill sharks in the region. Given the high level of transience, one might expect that the site may just happen to be along the path of the sharks as they move through the Bay. If this were the case, you would expect to find sharks in similar abundances and regularity at other locations in the range of the species. However, as there are no other reported sites displaying the level of abundance observed at the Pyramid Rock site, this explanation seems unlikely. Therefore, there must be something at this site in particular that draws individuals to it.

It is likely that the site is being used as a resting spot during the day. The complexity of the habitat, combined with barriers created by the kelp forest and large boulders, would offer shelter from predation during a time when these sharks are resting and relatively inactive. Evidence, in the

form of fresh scars on the flanks of large females, suggests that the site may also be used as a mating ground, although no observations of mating behaviour have been made to date. The high abundance of females at the site also suggests that the site may also act as a refuge for females wanting to avoid harassment from males, although the fact that large numbers of females can always be found at this site may detract from this hypothesis, as males looking to mate will know where to find females. Given that no observations of predation were observed at the site over the course of this study and the theory that these sharks are largely nocturnal predators, it seems unlikely that the use of this site is linked to foraging during the day. However, the possibility that the use of the site is related to foraging cannot be entirely disregarded, as night-time behaviours at the site have yet to be observed. Further work is required, including night observations (i.e. divers with spotlights, infra-red cameras, telemetry) and the inclusion of environmental factors (e.g. water temperature, currents, depth, oxygen levels), to determine the true factor, or combination of factors, attracting sevengill sharks to aggregate at this site.

This study also provides the first data on the fine-scale micro-habitat use of sevengill sharks in relation to the underlying substrata. Habitat preference appeared to be shown towards the interface between sand and rock habitats, with avoidance of areas with dense low-lying kelp and seaweed. If the site is being used as a resting area during the day, the complexity of the habitat should offer sufficient protection from predators without individuals needing to move through dense areas of kelp and seaweed, which may restrict their movements, reducing their ability to make a break from a predator in pursuit.

3.2 – Conservation

Habitat degradation is a common problem for coastal habitats, largely due to their close proximity to land and high human impact (Speed *et al.* 2010). As such, careful management is required to conserve the stability of coastal ecosystems.

As so many people survive off the oceans, whether through subsistence or commercial fisheries, it is impossible to protect the entire ocean. However, uncontrolled use of marine resources is unsustainable, therefore, restrictions are required to limit the effect of fisheries on marine ecosystems. Restriction can come in many forms, including size limits, bag limits and seasonal restrictions. One of the major tools at the disposal of marine managers it that of Marine Protected Areas (MPAs). MPAs place restrictions on a geographical scale, limiting the catch allowed in a particular area, and can range from protection for a single species to a complete no-take zone (Dulvy 2006). The advantage of an MPA is that it can be designed to protect particularly vulnerable zones (Fenberg *et al.* 2012), such as nursery areas, to allow for the recovery of stocks that are depleted outside of the protected area. The difficulty, however, lies is deciding on which areas to protect, finding a balance between the requirements of thousands of different species. The placement of an MPA must therefore consider the relative threats facing each species, and determine which species require the greatest protection. To do this, research is required to determine the resilience of a species to man-made threats, as well as the areas that are vital to different life stages of the species.

The Pyramid Rock site examined for this study falls within the Table Mountain National Park (TMNP) MPA (Figure 2.2). While the reserve stretches from Muizenburg in False Bay to Greenpoint, west of the Peninsula, only small areas within this reserve are classed as restricted, no take zones, one of which is the Castle Rock Restricted Zone, in which the Pyramid Rock site is located. This means that the site is a complete no take zone, supposedly offering complete protection from human impact (although lack of enforcement means some level of fishing can occur). If the site is indeed being used as a mating or pupping ground for sevengill sharks, this protection may play an important role in the life cycle of the species. The TMNP MPA was established in 2004 and there is already evidence for a positive effect on sevengill sharks. A survey of reef fishes carried out at the site in 2002 (Lechanteur& Griffiths 2002), prior to the establishment of the TMNP MPA, made only two observations of sevengill sharks over the duration of the study. In addition to this, anecdotal evidence from other divers suggests an increase in the number of individuals at the site. Stories from

divers who frequented the site 20 years ago tell of only ever encountering one or two sevengill sharks on a dive (Cliff pers.com.). Another account suggested that there was a resident shark at the site, sighted frequently, but never with more than one or two other sharks. Even as recently as 2008, divers have reported high levels of seasonality, with no sharks ever sighted during winter. These accounts seem to contrast current findings, suggesting a marked increase in the number of sharks at the site in recent years and that the TMNP MPA may have produced positive results for sevengill sharks. The increase in the number of sevengill sharks taken by demersal fisheries (DAFF 2010) suggests that these increases in shark numbers are not a result of reduced fishing pressure.

The aggregation of sevengill sharks at Pyramid Rock also shows potential for conservation in the form of eco-tourism. While not only providing revenue for the country, eco-tourism plays a vital role in educating the public. Sharks generally have a bad reputation in the public eye, with sensational movies such as the 1975 film, Jaws, instilling fear in the public. Even nature documentaries, supposedly educational programs, often portray sharks as killers, sensationalizing attacks. Eco-tourism dives with sevengill sharks, on the other hand, allow members of the public to get up close and personal with these apex predators. The ability to dive with these potentially dangerous animals, without the need for bait or cages, allows people to realise that sharks are not the killers that the popular media makes them out to be, helping reduce the stigma about sharks, which will ultimately help in the conservation of not only sevengill sharks, but of all shark species.

3.3 – Shortcomings and future work

A major shortcoming of this project was the lack of size data gathered in the field. Data on the size of individuals can play an important role, shaping elements of population demographics. Different sized individuals may have different survival rates or different movement patterns relating to reproduction in mature individuals. Unfortunately, due to the methodology of this study, size information could not be determined from photographs without a reference scale. Attempts to include a scale in the image using a pole of known length held alongside the shark proved

unsuccessful. Another method that was considered is the use of a dual laser system attached to the camera, which projects two dots of a known distance apart onto the body of the shark, which can later be seen in the photographs. Given logistical restrictions on this project, this system was not acquired.

This study made use of civilian divers involved in sevengill shark eco-tourism. While there are some drawbacks relating to the use of civilian divers in the collection of data, there are also many advantages. A major advantages is, given the time restraints on researchers, trained civilian divers, in particular those involved in the tourism industry, can provide a useful means of data collection on a far more extensive scale than would be possible by a lone researcher. The use of civilian divers has proven to be successful in other marine studies, including extensive studies on whale sharks, *Rhincodon typus* (Arzoumanian *et al.* 2005, Meekan *et al.* 2006, Bradshaw *et al.* 2007), bull sharks, *Carcharhinus leucas,* from Fiji (Brunnschweiler & Baensch 2011) and raggedtooth sharks, *Carcharias tauras,* from Australia (Otway *et al.* 2003).

Dickinson *et al.* (2010), in a review on the use of civilian science as a research tool, list two major sources of potential bias when using civilian scientists to collect data. Firstly, there is the error due to observer quality, the concern being that the skill of participants is less than that of the professional biologists, creating greater potential for error, particularly when large numbers of volunteers are involved. This study, however, only made use of a select few divers for data collection, all of whom have some background in scientific research and were briefed extensively on the requirements of this problem. The potential bias due to observer quality is therefore limited in this case.

The second source of error comes from sampling bias. Variation in sampling effort in both time and space may lead to potential bias in the data. In the case of this study, a possible major bias in the use of citizen science is the variation in sampling effort in space. While the primary diver, Morné Hardenberg, is knowledgeable on scientific procedures and was briefed on the collection protocols,

the requirements of clients to see the maximum number of sharks on each dive would have resulted in the focus of dives being around known hotspots. The problem lies in whether the data at these hotspots are representative of the site as a whole. This may have resulted in bias in the habitat use findings.

The irregularity of dives is also a factor which should be considered. The schedule of dives was largely influenced by weather and sea conditions. Given the unpredictable nature of the environment, the times between sampling periods varied. As I included data collected during a pilot project done as part of my honours degree, there was a three month gap in data collection due to a break in sampling during the completion of my honours project. These irregularities may have had an influence on predictions of recapture probabilities as data were grouped together, however, models were able to account for these groupings and produce survival estimates which were unbiased.

PhotoID has been shown to be a suitable means to identify individual sevengill sharks and I would recommend the continued use of this method in future studies, although a double tagging system should be considered to validate the method (Dudgeon *et al.* 2008).While the use of photoID is a valuable tool for the study of the species, an extension of this project should consider the use of telemetry systems to gain insight into the areas being used by individuals once they leave the site, as well as to gather data on movement variables such as depth, speed and water temperatures.

Future studies would benefit from long term-observations, making use of regular sampling periods throughout the year to determine true estimates of seasonal patterns in abundance, survival and behaviour. The inclusion of size data should also be a priority.

Night observations should also be considered to determine the activities of individuals at the site at night. Given that the species is known to be nocturnally active, night observations may help fill the gaps relating to the use of the area. Night dives, however, carry a range of logistical

difficulties, including the need for adequate lighting and the possible dangers involved with diving with these potentially dangerous predators at night, when they are active. Due to these logistical issues, no night dives have been conducted as of yet. A possible alternative is the use of telemetry systems and infra-red camera, which will provide insight into the nocturnal behaviours of individuals at this site.

Chapter 6 – References

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